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SYSTEMATIC PLANT STUDIES

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and JOSEPH EWAN**



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FRANK A. TAYLOR,
Director, United States National Museum.

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U N I T E D S T A T E S N A T I O N A L M U S E U M

CONTRIBUTIONS FROM THE UNITED STATES NATIONAL HERBARIUM

VOLUME 35, PART 1

SUPPLEMENTAL NOTES ON THE AMERICAN
SPECIES OF PASSIFLORACEAE WITH
DESCRIPTIONS OF NEW SPECIES

By ELLSWORTH P. KILLIP



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SMITHSONIAN INSTITUTION • WASHINGTON, D.C. • 1960

Preface

This paper was partly prepared by Ellsworth P. Killip, 10 years after the publication of his monograph of the Passifloraceae in 1938, to summarize the additional data acquired in the 10-year period, and to present descriptions of 8 new species. In 1956, Mr. Killip turned over the manuscript to Dr. José Cuatrecasas to use as he saw fit in the preparation of a flora of Colombia. It is now published with the addition of three new species that Mr. Killip indicated as new but did not describe. Dr. Cuatrecasas wrote descriptions for these as well as Latin diagnoses for all the new species described by Mr. Killip. Included are 11 new species and citations of all new material examined since the publication of the monograph. Dr. Lyman B. Smith, curator of the division of phanerogams, has carefully edited the manuscript.

JASON R. SWALLEN

Head Curator, Department of Botany

SUPPLEMENTAL NOTES ON THE AMERICAN SPECIES OF PASSIFLORACEAE, WITH DESCRIPTIONS OF NEW SPECIES

By ELLSWORTH P. KILLIP

Introduction

In 1938 the Chicago Natural History Museum (then the Field Museum of Natural History) published a monograph on the American species of Passifloraceae written by the present author.¹ The preparation of this monograph covered a period of many years, during which time I made three visits to Europe and consulted nearly all the type specimens as well as many others of historic importance. A large amount of material was generously placed at my disposal by those in charge of many of the larger herbaria of the world. It is therefore perhaps not surprising that in the intervening years I found little reason to revise the treatment of the species presented in the monograph.

The intensive exploration carried on in certain parts of northern South America, especially in the basins of the Orinoco and Amazon in Colombia and Venezuela, resulted in the collecting of many Passifloraceae in regions little known in 1938. In the course of studying these specimens, as well as material from Central America and other parts of South America, I detected several new species, some of which I described elsewhere. This material also shows interesting extensions of ranges of certain species, and in some instances permits a desirable amplification of the descriptions given in the monograph. It therefore seems advantageous to assemble in one place all this subsequent information along with descriptions of several new species. The numbers associated with the species of *Passiflora* are those of the monograph.

4. *Passiflora gracillima* Killip

This species is now represented in the U.S. National Herbarium by several additional Colombian collections. One specimen from the

¹Field Mus. Bot. 19. 1938.

Province of Chiriquí, Panama, was cited; the species was recollected in the vicinity of Chiriquí Lagoon in 1941 by H. von Wedel (No. 2421). Likewise, a single specimen was listed from Riobamba, Ecuador. This species is now represented by *Steyermark* 52932, which was collected between Cruz Pamba and Loma de Canela, north of Molleturo, Province of Azuay, Ecuador, at an altitude of 2,315–2,500 m. The collector noted that the fruit is edible and has a flavor similar to that of *Annona*.

10. *Passiflora gracilis* Jacq.

Additional collections are:

VENEZUELA: Bolívar: Gran Sabana, Cerro Kanaimé Santa Elena, March 1946, *Tamayo* 3025.

ECUADOR: Azuay: Between Río Gamolotal and Río Norcay, *Steyermark* 52879.

Both of these collectors noted that the fruit is red. Steyermark gave "shunshun" as a local name, and stated that the corona filaments are white with a purple streak at the center and that the seeds are red.

14a. *Passiflora ursina* Killip & Cuatr., sp. nov.

PLATE 1

Frutex elatus scandens; rami foliosi dense rufo-tomentosi; stipulae subulatae; folia coriacea trinervia ovato-oblonga vel oblonga basi truncata vel rotundata apice acuta vel subacuta mucronulata utroque latere saepe 1-lobata, lobo triangulari brevi mucronulato, subtus rufo-hirtella vel tomentella, margine integra revolutaque, petiolo brevi basi duobus glandulis minutis inconspicuis; bractae liberae subulatae; calycis tubus petalliformis, sepalis ovatis apice rotundatis subapicem corniculatis, petalis paulo brevioribus; corona filamentis biseriatis apice incrassatis exterioribus robustioribus; operculum membranaceum plicatum erectum breviter fimbriatum; ovarium glabrum.

Large, scandent shrub; leafy branches moderately thin, flexuose subterete, densely reddish brown tomentose with acute, subrigid, spreading hairs, 0.5–1 mm. long; tendrils closely spiral, tomentose; stipules subulate, hirsute, 5–6 mm. long, 0.5–1 mm. broad; petioles 8–14 mm. long, stout, straight or bent at base, densely rufo-tomentose (like the branches), the glands small, semiglobular, sessile at base, concealed by the indument; blades coriaceous, trinerved, ovate-oblong or oblong, 5–8.2 cm. long, 3–4.5 cm. broad, rounded, truncate or cordate at base, subtrilobate (or rarely entire) near the apex, the two lateral lobes very short, forming an obtuse mucronulate angle, the terminal one (the apex) acute or subacute, mucronulate, the margin entire, revolute, the surface puberulous with spreading, sparse hairs

above, pubescent or subtomentose with spreading, long, rufous hairs beneath, the 3 nerves and veins very prominent beneath, little conspicuous above; a few minute, semiglobose glands near the base beneath; inflorescence cymose, the cymes in pairs with 5–7 flowers, the rachis less than 1 cm. long; bracts subulate, 3–5 mm. long, up to 0.5 mm. broad, rufo-hirsute; the peduncles thick, straight, rufo-tomentose, 8–14 mm. long, articulate about the middle or slightly above the middle; flowers 2.5–3 cm. wide, greenish white; sepals ovate, obtuse, 1.1–1.3 cm. long, 0.7–0.9 cm. wide, dorsally more or less hirsute and keeled, corniculate below the apex, the horn up to 3 mm., hairy; petals membranaceous, ovate, narrowed at both ends, obtuse, subdentate below the apex, 1–1.1 cm. long, 0.6–0.7 cm. wide; corona filaments filiform, much dilated at apex, in 2 series, the outer about 3.5 mm. long, rigidulous, the inner about 2.5 mm. long, thinner and flexuose; operculum membranaceous, closely plicate, short-fimbriate, 1.5 mm. high; limen annular; gynophore absent; ovary ellipsoid-obovoid, glabrous.

Type in the U.S. National Herbarium, No. 1799118, collected at Páramo de Santa Lucía, south side of Laguna de la Cocha, Department of Nariño, Colombia, at an altitude of 2,900–3,100 m., on Jan. 9, 1941, by J. Cuatrecasas (No. 11886).

P. ursina is closely related to *P. apoda* Harms and *P. sodiroi* Harms, from which it differs in the thick, longer, rufous indument, in the shorter petioles with sessile, minute basal glands concealed by the indument, and more conspicuously in the horned sepals. It differs from *P. sodiroi* in lacking the gynophore and in the form of the petals, and from *P. apoda* by the shorter corona filaments.

26. *Passiflora dolichocarpa* Killip

Known only from the type specimen at the time of my monograph, this species is now represented in the U.S. National Herbarium by the following additional collections:

MEXICO: Chiapas: Hacienda Siltepec, *Matuda* 1892.

GUATEMALA: Jalapa: Between Jalapa and Montaña Miramundo, alt. 1,500–2,000 m., *Steyermark* 32884 (F). Suchitepéquez: Volcán Santa Clara, alt. 1,250–2,650 m., *Steyermark* 46761.

46a. *Passiflora macrostemma* Killip, Field Mus. Bot. 23:217. 1947.

Additional collections are:

GUATEMALA: Chiquimula: Volcán de Quezaltepeque, alt. 1,500–2,000 m., *Steyermark* 31519 (F, type, US photo and fragment), 31281 (F). Jalapa: Montaña Durazno, alt. 1,400–1,900 m., *Steyermark* 32985 (F).

61. *Passiflora lancearia* Mast.

Recorded as being confined to Costa Rica, this species was collected in the Province of Chiriquí, Panama, in 1938 by M. E. Davidson (No. 336) and in the Province of Bocas del Toro in 1941 by H. von Wedel (No. 2120).

63. *Passiflora panamensis* Killip

This species was known at the time of my monograph only from the type, which came from southern Darién, Panama. The species has been found in the adjacent coastal part of Colombia, a recent record being:

COLOMBIA: El Chocó: Bahía Solano, dense forest along the Quebrada Jellita, alt. 50-100 m., Feb. 22, 1939, *Killip & García* 33482.

69. *Passiflora bauhinifolia* H.B.K.

P. andreana Mast. was treated as a synonym of *P. bauhinifolia* in my monograph. Specimens collected by García-Barriga and Balls in southwestern Colombia in 1939 show that these two species are unquestionably distinct. In *P. andreana* the inside of the sepals and the petals are purple, reddish purple, or deep violet; in *P. bauhinifolia* these parts are white. The outer corona filaments are slenderer in *P. andreana*.

Of the specimens listed in my monograph under *P. bauhinifolia*, I have rechecked only those in the U.S. National Herbarium; on this basis, *P. bauhinifolia* is common in Ecuador, and *P. andreana* is known only from Colombia. *P. bauhinifolia* is represented in the U.S. National Herbarium by the following:

COLOMBIA: El Valle: Quebrada de la Palma, Río Bugalagrande Valley, *Cuatrecasas* 20935. Putumayo: Laguna de la Cocha, Páramo El Tabano, *García-Barriga* 7785A.

ECUADOR: Without locality, *Mille*. Imbabura: Otovalo, *Mexía* 7645. Pichincha: Quito, *Humboldt & Bonpland* (photo of type); *Mille* 222, s.n. in 1918. Verde Cruz, *Firmin* 310. Guápulo, *Stevens* 258. Tungurahua: Baños, *Lehmann*, 675, 8020.

PERU: Cajamarca: Peña Rota, toward Cochabamba 2,800 m., *Ochoa* 1565.

This last record is apparently the second of this species in Peru.

69a. *Passiflora andreana* Mast. Journ. Linn. Soc. 20:37. 1883.

Additional collections are:

COLOMBIA: Nariño: Las Lajas, near Ipiales, *André* 3478 (photo of type); *García-Barriga* 7757A; *Balls* 7360. Jenoy, 5 km. northwest of Pasto, alt. 2,460 m., *Ewan* 15899 (USNA). Between Pasto and Anganoy, *Schultes & Villarreal* 7417.

100. *Passiflora micropetala* Mast.

In the monograph I stated that this species was one of the few maintained as valid by Masters in the *Flora Brasiliensis* that I knew only from description. After studying a specimen subsequently collected along the Río Putumayo, I have decided that it and a specimen from the Comisaría of Caquetá, *Pérez-Arbeláez* 669, which was cited by me as *P. dawei*, both represent *P. micropetala*. The type locality of this species as given by Masters is: "In regione fluvii Japurá, prov. do Alto Amazonas." The Río Japurá is identical with the Río Caquetá, and the Putumayo is in the same general area. On his trip to this river, Martius is known to have collected in present-day Colombia, and the type may thus have come from this country.

The Pérez collection is sterile, and the more recent one is in fruit only. Both resemble *P. biflora* in leaf shape, but the coronal structure is different according to Masters' description. *P. micropetala* therefore appears to be known from the following locations:

COLOMBIA: Caquetá: Florencia, alt. 420 m., *Pérez-Arbeláez* 669 (COL, US).

Putumayo: Selva higrófila del Río Putumayo en Puerto Ospina, alt. 230 m., *Cuatrecasas* 10776 (COL, US).

BRAZIL or COLOMBIA: Río Japurá (R. Caquetá), *Martius* (M, type).

111. *Passiflora adenopoda* DC.

A recent collection of this species by Dugand and Jaramillo (No. 3965) has far more deeply cleft bracts than heretofore observed. They are deeply palmate-trisect, and the segments are repeatedly cleft. The largest bract is 2 cm. wide. This unusual variant was collected in the Department of Cundinamarca, Colombia, at Estación San Bernardo, between Sasaima and Albán, at an altitude of 1,700–1,800 m.

132. *Passiflora bicuspidata* (Karst.) Mast.

This species, known hitherto only from the Eastern Cordillera of Colombia, was recently collected by Steyermark across the border in Venezuela. His detailed notes on the color of the flowers are worth reproducing as earlier collectors have described the flower color in only general terms.

"Calyx rose-lavender, the lobes with more lavender, the tube with more brick-color; coronal filaments golden; calyx tube below the coronal filaments within dull pale greenish-yellow; filaments purple; anthers buff; styles purplish; petals purplish-rose."

The collection was made at:

VENEZUELA: Táchira: Swampy woods between Paramito and Quebrada de Palmar, at base of Páramo de Tamá, 7 km. above Villapáez, alt. 2,500 m., *Steyermark* 57240 (F, US).

135. *Passiflora sanguinolenta* Mast.

In the monograph I followed Masters in placing this Ecuadoran species in the subgenus *Psilanthus*, but I observed that it appeared more closely related to *P. rubra*, of the small section *Xerogona* of the subgenus *Plectostemma*, than to the three known species of *Psilanthus*.

Later, there were submitted to me, through the courtesy of Harold N. Moldenke, then of the New York Botanical Garden, a fine series of specimens of *P. sanguinolenta* and *P. rubra* collected by Reinaldo Espinosa in the Province of Loja. One of *P. sanguinolenta*, No. 806, is in fruit, apparently the first time that fruit of this species has been collected. The transverse ridges of the seeds are rugose, not smooth as in *Xerogona*, and I believe that the species is best left in *Psilanthus*, even though in vegetative parts (especially in the absence of any bracts) and shape of the fruit it very closely resembles *P. rubra*.

To the collections cited in the monograph there may now be added the following, all from the Province of Loja and deposited in the U.S. National Herbarium:

ECUADOR: Catacocha, alt. 2,050 m., *Espinosa* 617. Pucala, north of Loja, alt. 2,300 m., *Espinosa* 621. Between San Pedro and Chinchas, about 55 km. west of Loja, alt. 1,200 m., *Espinosa* 1314. Aguahedionda, north of Loja, alt. 2,150 m., *Espinosa* 806. Desert country between Vilcabamba and Cachiyaçu, alt. 1,600–2,100 m., *Steyermark* 54397.

137. *Passiflora bracteosa* Planch. & Linden

Tacsonia infundibularis Mast.

Both these species were based upon *Funck and Schlim's* 1381. The type locality of *P. bracteosa* was correctly given as La Baja, Colombia; that of *Tacsonia infundibularis* was incorrectly recorded as "Venezuela." However, this species has recently been collected by Steyermark (No. 57277, at F) in the State of Táchira, Venezuela, at the base of the Páramo de Tamá, at an altitude of 2,285–2,430 m.

147. *Passiflora adulterina* L.f.

Although this species is fairly common in the vicinity of Bogotá, fruiting material was not found, apparently, until 1939. *Cuatrecasas* 5136, collected between El Delirio and Guadalupe (eastern slope of the Cordillera Oriental, between 2,900 and 3,220 m. altitude), bears mature fruit, which may be described as follows:

Fruit broadly ovoid, 7.5 cm. long, about 4.5 cm. in diameter, apparently reddish brown, mottled with greenish yellow; seeds obovate, about 9 mm. long, and 4.5 mm. wide, reticulate, dark brown, lustrous.

148a. *Passiflora cuatrecasatii* Killip, sp. nov.

PLATE 2

Suffrutex elata scandens, caule primum lanato denique glabrato; stipulae subulatae; folia coriacea ovato-lanceolata vel oblongo-lanceolata plus minusve serrata basi rotundata vel subcordata apice acuta vel subobtusa subtus lanata, petiolo sub apice 2–3 glandulis; bracteae liberae ovato-oblongae vel anguste oblongae acutae serrulatae; calycis tubus cylindricus glaber, sepalis tubo valde brevioribus oblongis obtusis, petalis sepala subaequalibus; corona annularis undulata; operculum deflexum denticulatum leviter recurvatum; ovarium tomentosum.

Vine; stem subangular, lanate when young, the indument at length evanescent; stipules subulate, up to 1.1 cm. long, glabrous, purplish black below middle, the upper part spongiose-thickened, light yellowish brown, coriaceous, acuminate; petioles up to 2 cm. long, bearing 2 or 3 glands near apex; leaves unlobed, ovate-lanceolate or oblong-lanceolate, 6–11 cm. long, 3–6.5 cm. wide, acute or subobtuse, rounded or cordulate at base, serrate or serrulate, penninerved (principal lateral nerves about 9 to a side), coriaceous, dark green, lustrous, and glabrous above, densely lanate beneath, except sometimes on the nerves and veins; peduncles 7–10 cm. long, slender, evanescently lanate, articulate about 1 cm. below the apex; bracts distinct to the base, ovate-oblong to narrowly oblong, 3–4 cm. long, 0.8–3 cm. wide, acute, sessile, finely serrulate; calyx tube cylindric, 8–10 cm. long, 1–1.5 cm. wide, greenish at base, red or purplish above, glabrous; sepals oblong, 3.5–4.5 cm. long, 1–1.5 cm. wide, obtuse, dorsally awned just below the apex (awn about 1.5 mm. long), pinkish purple; petals subequal to the sepals; corona a single indulate ridge at the apex of the tube; operculum borne near the base of the tube, 4–7 mm. long, dependent, the margin slightly recurved and minutely denticulate; ovary ovoid, densely tomentose.

Type in the U.S. National Herbarium, No. 1796435, collected on the eastern slope of the Páramo de Guasca, Cordillera Oriental, Department of Cundinamarca, Colombia, at an altitude of 3,200–3,300 m. on June 2, 1940, by J. Cuatrecasas (No. 9479). Also represented by *J. Cuatrecasas* 13538 from the same locality, and by *Uribe* 1061, from La Rusia, northwest of Duitama, Department of Boyacá, at an altitude of 2,700 m.

The proposed species probably should be placed nearest *P. lanata* in the arrangement adopted in my monograph, though it also has affinities with *P. rugosa* and *P. leptomischa*. From *P. lanata* it differs in having a scantier indument on the vegetative parts, a pubescent ovary, and generally longer peduncles. In *P. rugosa* the bracts are coalesced partway and the calyx tube is much shorter. *P. leptomischa* is a species with dimorphic foliage and very long (15–25 cm.) peduncles.

148b. *Passiflora rigidifolia* Killip sp. nov.

PLATE 3

Caulis scandens angulatus sursum albopilosus basin versus glabratus; stipulae anguste lineares glanduloso-serrulatae subrevolutae; folia coriacea lanceolata integra basi rotundata apice acuta praeter costam supra pilosulam glabra, petiolo albo-piloso 2-3 glandulis parte media; bracteae liberae lanceolatae integrae; calycis tubus cylindricus glaber sepalis tubo brevioribus oblongis obtusis, petalis sepalis similibus; corona annularis dentata; operculum deflexum recurvatum minuteque denticulatum; ovarium tomentosum.

Stem subangular, white-pilose toward the apex, becoming glabrous below; stipules narrowly linear about 1 cm. long and 1 mm. wide, acuminate, glandular-serrulate, subrevolute, coriaceous; petioles up to 7 mm. long, 2- or 3-glandular near the middle, white-pilose; leaves lanceolate, 4-6.5 cm. long, 1-1.8 cm. wide, acute at apex, rounded at base, entire, revolute (?), penninerved (midnerve impressed above, the lateral nerves and veins somewhat elevated on both surfaces), pilosulous on the midnerve above, otherwise glabrous, coriaceous, glaucescent beneath; peduncles solitary in the axils, 2-2.5 cm. long, glabrous or sparingly pilose; bracts borne about 5 mm. below the apex of the peduncle, free to base, lanceolate, about 2 cm. long and 8 mm. wide, acuminate, sessile, entire, pilose; flowers pale rose; calyx tube cylindric, 6.5-7 cm. long, 8-9 mm. in diameter, slightly enlarged at base, glabrous; sepals oblong, about 2.5 cm. long, and 1 cm. wide, obtuse, dorsally aristate just below apex, the awn 2 mm. long; petals similar and subequal to the sepals, about 8 mm. wide; corona a dark ring at the throat of the tube, tuberculate; operculum borne close to base of tube, 4 mm. long, dependent, the margin recurved and minutely denticulate; ovary ovoid, densely tomentulose.

Type in the Herbarium of the Royal Botanic Gardens, Kew, collected in Colombia at an altitude of about 3,900 m., 1894-1896, by D. Burke (No. 184).

This species is nearest to *P. cuatrecasasii* but differs in its much narrower leaves, shorter peduncles, and slenderer calyx tube.

Unfortunately, the locality at which the type was collected is uncertain. The label reads "Flora of Colombia. Locality: Conig, altitude 13,000 ft., Comm. Messrs. J. Veitch, 1897." The word "Conig" is not a Spanish one, and I have been unable to find in any gazeteer a Colombian name at all similar to it. Conejo, in Antioquia, on the railroad from Puerto Berrío to Medellín, suggests itself, but there is no altitude of 13,000 ft. attainable from there. In Peru there is a "Coñec," but it is not known that Burke collected in that country.

Accompanying this specimen is a letter dated April 4, 1902, from James Veitch & Sons to Hemsley, in response to a request for information about Burke's collections. Nos. 146, 154, and 167 are listed

without localities, but the Veitch letter observes that the preceding numbers were collected in Antioquia. Nos. 184 and 185 follow both from "Conig," number 185 being given as "*Berberis* sp (*Goudoti* ?), 11,000 ft." *Berberis goudoti* is known only from the eastern Cordillera of Colombia.

149. *Passiflora truxillensis* Planch. & Linden.

This rare species hitherto known only from two collections from the State of Trujillo, Venezuela, was recently collected in the neighboring State of Mérida by Steyermark, from whose notes the following more complete description of the flowers may be presented:

Bracts pale green with pale rose line down the center; calyx tube pale green at very base, dull rose without, a greenish part in the middle; sepals deep rose at margin, lavender in the middle; petals rose-colored throughout; stamen-filaments rose-orchid; ovary green; styles rose-lavender above, whitish below.

The complete collection data are:

VENEZUELA: Mérida: Rich forest between Mesa del Trapiche and El Molino, alt. 2,530–2,590 m., *Steyermark* 56503 (F, US).

154a. *Passiflora boyacana* Killip sp. nov.

PLATE 4

Herba scandens, caule lanato denique glabrescenti; stipulae lineari-subulatae; folia coriacea profunde trilobata basi subtruncata vel subcordata lobis lineari-lanceolatis subacutis mucronulatis integris, subtus dense rufo-lanata, petiolo eglanduloso lanato; bracteae liberae integrae extus lanatae; calycis tubus cylindricus glaber, sepalis petalisque tubo dimidio brevioribus elliptico-oblongis obtusis mucronulatis; corona brevem annulum minute tuberculatum reducta; operculum deflexum recurvatum denticulatum; ovarium glabrum.

Herbaceous vine; stem stout, subterete, about 3.5 mm. in diameter, lanate, becoming glabrous; stipules linear-subulate, about 1.2 cm. long; petioles 1–1.5 cm. long, glandless, lanate in lines; leaf-blades lobed about three-quarters their length, 4–8 cm. along midnerve, 3.5–6.5 cm. along lateral nerves, 3–9 cm. between apices of lateral lobes, (lobes 1–1.5 cm. wide, narrowly lanceolate or the middle one sometimes elliptic-lanceolate, subacute, mucronulate), subtruncate or cordulate at the base, entire, coriaceous, essentially glabrous above with the nerves slightly impressed, densely rufo-lanate beneath; peduncles solitary, about 4 cm. long, pubescent like the petioles; bracts borne at base of flower, 2–2.3 cm. long, 8–10 mm. wide, free to the base, sessile, entire, deciduous-lanate without, glabrous within; flowers young; calyx tube cylindric, 4 cm. long, glabrous; sepals and petals equal, about 2 cm. long, obtuse, the sepals 7 mm. wide, mucronulate, the petals 1 cm. wide; corona reduced to a low, minutely tuber-

culate ridge; operculum borne at base of tube, dependent, about 4 mm. long, the margin recurved, denticulate; ovary ellipsoidal, glabrous.

Type in the U.S. National Herbarium, No. 1796049, collected in páramo thickets, above Puente de Boyacá, Department of Boyacá, Colombia, at an altitude of 2,800 m. on Feb. 24, 1940, by E. Pérez-Arbeláez & J. Cuatrecasas (No. 8083).

This species, belonging to the subgenus *Tacsonia*, keys out to species 154–157 of my monograph of the American Passifloraceae. The narrow, entire leaf lobes are quite unlike those of *P. ampullacea*. In depth of lobation the leaves are rather suggestive of *P. trianae* and *P. purdiei*, which are essentially glabrous plants.

155a. *Passiflora raimondii* Killip, sp. nov.

PLATE 5

Herba scandens, ubique glabra; stipulae setaceae; folia membranacea trilobata, lobis oblongis vel ovato-oblongis, obtusis, denticulatis, petiolis eglandulosis; bracteae liberae, lanceolatae, acutae; calycis tubus cylindricus, sepalis tubo brevioribus, lineari-oblongis, petalis anguste linearibus; corona annuliformis, crenulata; operculum deflexum.

Herbaceous vine, glabrous throughout; stem quadrangular, longitudinally ridged, the tendrils very slender; stipules setaceous, about 4 mm. long; petioles slender, 1–3 cm. long, glandless; leaves 3–5 cm. long, 4.5–8 cm. wide, 3-lobed to below the middle (lobes oblong or ovate-oblong, up to 3 cm. wide, rounded and sometimes slightly emarginate at apex, denticulate), cordate at base, membranous, biglandular at base; peduncles solitary, slender, about 5 cm. long; bracts lanceolate, 1–1.2 cm. long, 4–5 mm. wide at base, acute at apex, rounded at base, sessile, minutely denticulate, distinct to base, borne at base of flower; calyx tube cylindric, 3–3.5 cm. long, 7–8 mm. in diameter, narrowed at base; sepals linear-oblong, 2 cm. long, 3–3.5 mm. wide, obtuse, slightly carinate, the keel terminating in a filiform awn 1 mm. long; petals narrowly linear, 1.5 cm. long, 1.5 mm. wide, subacute; corona a low ridge, crenulate; operculum borne about 5 mm. above base of tube, dependent, 4 mm. long, minutely denticulate; gynophore very slender, about 5 cm. long; ovary fusiform.

Type in the Herbarium of the Universidad Nacional Mayor de San Marcos, Lima, collected at Chorrillos, Department of Cajamarca, Peru, at an altitude of 2,200 m. on June 8, 1875, by A. Raimondi (No. 7807). Represented also by *A. Raimondi* 8241, collected at Cascas, Province of Contumazá, in the same Department.

This species is most nearly related to *P. gracilens*, which is rather common in Peru and extends from Huánuco southward. The new species differs in its larger leaves with much broader lobes, its longer peduncles and larger flowers, and its lanceolate, not ovate, bracts.

The Raimondi specimens were submitted to Harms, who suggested that they probably belonged to our undescribed species.

159a. *Passiflora zamorana* Killip sp. nov.

PLATE 6

Herba scandens folia supra et flores excepti dense griseo-vel brunneo-tomentosa; stipulae late ovato-reniformes semiamplexicaules plus minusve dentatae vel incisae; folia membranacea usque medium 3-lobata basi subcordata lobis oblongo-lanceolatis argute acuminatis serratis supra pilosula deinde glabrata, petiolo 3-4 glandulis inconspicuis praedito; bractae liberae ovato-lanceolatae serrulatae; calycis tubus cylindricus glaber, sepalis petalisque ovato-oblongis obtusis tubo paulo brevioribus; corona circulum minorum tuberculorum reducta; operculum deflexum recurvatum; ovarium brunneosericeum.

Herbaceous vine, densely brownish or grayish tomentose throughout except the upper side of the leaves and the flowers; stem terete; stipules broadly ovate-reniform, about 1 cm. long and 1 cm. wide at the base, scarcely oblique, closely semiamplexicaul, irregularly dentate or lacinate at the apex, the divisions aristate; petioles 2-2.5 cm. long, bearing 3 or 4 obscure glands; leaves 6-9 cm. long, 8-9 cm. wide, 3-lobed about to the middle (lobes oblong-lanceolate, 2.5-3.5 cm. wide, sharply acuminate, the lateral somewhat ascending), conspicuously serrate, subcordate, membranous, the upper surface sparingly pilosulous glabrate; peduncles 12-15 cm. long, rather stout; bracts free to base, ovate-lanceolate, about 3 cm. long, and 1.7 cm. wide, acuminate, serrulate, sessile, borne at the apex of the peduncle; calyx tube cylindric, 7-7.5 cm. long, 1-1.3 cm. wide when pressed flat, slightly enlarged at base, otherwise of uniform diameter, glabrous; sepals ovate-oblong, 6-6.5 cm. long, about 2.5 cm. wide, obtuse, dorsally awned just below the apex (awn very slender, about 5 mm. long), deep salmon-rose, paler within, the midnerve with a pale green center; petals similar and subequal to the sepals; corona a single series of minute tubercles; operculum borne near the base of the tube, about 3 mm. long, dependent, the margin recurved; ovary ovoid, densely light-brown-sericeous.

Type in the Herbarium of the Chicago Natural History Museum, No. 1204733, collected in the vicinity of Achupallas, Province of Santiago-Zamora, Ecuador, at an altitude of 2,500 m. in a forest along a stream on October 8, 1943, by Julian A. Steyermark (No. 54493). Duplicate at US.

In the monograph the new species keys out to *P. jamesonii* because of the large stipules; however, these are far more deeply fringed in *P. jamesonii*. Moreover, *P. jamesonii* is glabrous throughout and has shorter peduncles and deeply fringed bracts. In leaf shape, indument, and length of the peduncles, the new species suggests *P. ampullacea*.

162. *Passiflora matthewsii* (Mast.) Killip

Masters placed this species among the *tacsonias* with united bracts, lobed leaves, and narrowly linear stipules, though in the description of the species, which was given at some length in the key, he did not specifically mention the stipules. A specimen recently collected at the type locality, Chachapoyas, Peru, by Metcalf (Goodspeed Expedition No. 30784) has foliaceous, semiovate stipules which are deeply pinnatisect into filiform segments, the body of the stipules sometimes being reduced to a mere band surrounded by the filiform segments. Otherwise the specimen agrees perfectly with a photograph that I took of the type at the Kew Herbarium and with the amplified description given in my monograph. I believe that both Masters and I mistook either the filiform segments or abortive tendrils for stipules, that the stipules of *P. matthewsii* had mostly fallen off the type material at Kew and the British Museum, and that therefore *P. matthewsii* should be placed next to *P. roseorum* (species 164).

A. H. G. Alston has kindly examined for me the Matthews specimen at the British Museum, and writes: "The stipules appear to have fallen off our specimen, but there are sometimes young tendrils which could easily have been taken for stipules. . . . On the young parts there are, however, some filiform hairy segments, which could easily be the segments of a laciniate stipule."

166a. *Passiflora loxensis* Killip & Cuatr., sp. nov.

PLATE 7

Suffrutex scandens, caule angulato glabro; stipulae coriaceae ovatae fimbriato-dentatae; folia coriacea glabra trilobata lobis triangulari-ovatis acutis serratis, subtus reticulo venorum valde elevato congesteque incrassato; bracteae ad medium connatae; calycis tubus cylindricus glaber, sepalis petalisque oblongis tubum subaequilongis; corona tuberculata; operculum deflexum paulo laciniatum recurvatum; ovarium glabrum.

Vine; stem acute-angular, glabrous, lustrous; stipules coriaceous, glabrous, ovate or lance-ovate, acuminate, oblique and cordate at base, amplexicaul, fimbriate-dentate, 10–20 mm. long, 4–8 mm. broad; petioles 1–2 cm. long, bearing 3–4 sessile or short-stipitate glands about 1 mm. thick; leaf-blades 4–6 cm. long, 5.5–9 cm. broad, deeply 3-lobed (lobes triangular-ovate, acute, 2–3.5 cm. long, 1.5–2.8 cm. wide, the lateral ones subascending), truncate or subrounded at base, callous-serrate, coriaceous, glabrous, above green, rugulose, the nerves impressed, the minute reticulate veins prominulous, beneath paler, the 3 primary nerves thick and prominent, the secondary nerves prominent, the veins thick forming an incrassate reticulum separating very narrow, deep, irregular alveolae; peduncles 2.5–4.5 cm. long, subangular, stout; bracts subcoriaceous, 5–6 cm. long, connate to

about the middle (the free part oblong, abruptly acuminate, entire, 1.4–2 cm. wide), outside glabrous, slightly nervate and reticulate, inside more or less lanuginous or pilose and conspicuously venose; flowers lilac-blue; calyx tube cylindric, 7–8 cm. long, about 1 cm. broad when pressed, of uniform diameter, glabrous; sepals oblong, obtuse, aristulate below the apex, 6.5–8 cm. long, 1.8–2.6 cm. wide; petals subequal to the sepals; corona tuberculate; operculum dependent, about 7 mm. long, the margin recurved, more or less fimbriate; gynophore finely spreading-pubescent; ovary fusiform, glabrous; immature fruit obovoid-oblong, about 6.5 cm. long, 2 cm. broad; seeds oblong-ovate, $7-8 \times 4-5$ mm., alveolate.

Type in the U.S. National Herbarium, No. 1909202, collected at Horta-Naque, Province of Loja, Ecuador, at an altitude of 3,200 m., on Nov. 8, 1946, by Reinaldo Espinosa (No. E965). Supplementary sheet, US No. 1909586.

P. loxensis belongs to the subgenus *Tacsonia* and is closely related to *P. cumbalensis* (Karst.) Harms. It differs in the laciniate-dentate, coriaceous stipules, in the more coriaceous leaves and bracts, and especially in the structure of the lower surface of the leaves. The thick veins on the lower surface form a very close reticulum that leaves very thin but deep and irregular pits between the turgid network.

170. *Passiflora psilantha* (Sodirol) Killip

This Ecuadorean species has been found in cultivation near Sonsón, Antioquia, Colombia, by Gutiérrez & Barkley (No. 18C294). The specimen is deposited in the Herbarium of the Facultad de Agronomía, Medellín, Colombia.

173. *Passiflora mixta* L.f.

On page 297 of my monograph, variations of pubescence in this wide-spreading species are noted thus:

- (1) Leaves, calyx tube, and ovary glabrous.
 - (2) Leaves glabrous, calyx tube and ovary pubescent.
 - (3) Under surface of leaves, calyx tube, and ovary pubescent.
- No formal varietal names were assigned to these variants though a fourth, *P. mixta* var. *eriantha*, was treated as a variety.

Two specimens received subsequent to the publication of my monograph exhibit other combinations in the occurrence of indument, and are worth noting:

- (4) Under surface of leaves pubescent, calyx tube glabrous, ovary pubescent: Ecuador: Cañar: Tipococha, altitude 3,200 m., *Penland & Summers* 1006 (US).

- (5) Leaves and calyx tube glabrous, ovary pubescent: Bolivia: La Paz: Charazani, Province of Muñecas, altitude 2,700 m., *Cárdenas* 3886 (US).

177. *Passiflora antioquiensis* Karst.

In the description given of this species in my monograph, notes on the peduncle were unfortunately omitted. It is worthwhile also to amend the description in certain details in view of recent collections thus:

Leaves unlobed, up to 18 cm. long and 8.5 cm. wide, asymmetrically 2-lobed or 3-lobed to within 2 cm. of the base; peduncles very slender, almost filiform, 17–60 cm. long, pendulous; flowers up to 14 cm. wide when expanded.

Additional specimens examined are:

COLOMBIA: Antioquia: Yarumal, *Daniel* 1916 (US). Cauca: El Tambo, alt. 2,500 m., *von Sneidern* 1442 (S,US).

180a. *Passiflora macropoda* Killip sp. nov.

PLATE 8

Caulis scandens robustus rufo-subvelutinus; stipulae cordato-ovatae acutae inciso-fimbriatae glabrae; folia subcoriacea pilosula ad medium trilobata basi subcordata lobis ovatis acutis serratis; bractae liberae ovato-lanceolatae subcordatae inciso-fimbriatae; calycis tubus tubuloso-campanulatus, sepalis anguste lanceolatis pilosulis apice longe mucronatis quam tubo duplo longioribus, petalis leviter brevioribus; corona 3 seriebus filamentis filiformibus et interiore brevi membrana horizontali subcrenata; operculum deflexum recurvum; gynophorum tener; ovarium velutinum.

Vine; stem terete, stout, about 5 mm. in diameter, rufo-velutinous; stipules cordate-ovate, 2–3 cm. long, 1.5–2 cm. wide, acute, strongly oblique at the base, laciniate-fimbriate, membranous, glabrous; petioles stout, 1.5–3 cm. long, bearing 2 or 3 short stipitate glands at the apex and 1 or 2 just below the apex, these partially concealed in a dense tomentum; leaf-blades 3-lobed about to middle, 10–12 cm. along the midnerve and the lateral nerves, 16–18 cm. between the apices of the lateral lobes (lobes about 5 cm. wide, aristate), cordulate at base, serrulate, subcoriaceous, minutely pilosulous on the nerves above and on the principal nerves beneath cano-puberulent or rufo-puberulent on the secondary nerves and the veins beneath; peduncles solitary, stout, 12–14 cm. long, densely rufo-velutinous; bracts free to base, ovate-lanceolate, 4–5 cm. long, about 2 cm. wide, cordulate, laciniate-fimbriate, the teeth toward the base the largest; calyx tube slenderly campanulate, about 2 cm. long, and 1.3 cm. in diameter; sepals narrowly lanceolate, 4 cm. long, 1 cm. wide, white within, dorsally keeled toward the apex, the keel terminating in a filiform awn about 8 mm. long; petals narrowly lanceolate, 3.5–4 cm. long, white; corona in 4 series, the outer 3 ranks irregular, filamentose, the filaments filiform, about 1.5 cm. long, close to these ranks a short, thick, horizontal, subcrenulate membrane; operculum dependent,

about 8 mm. long, the margin recurved, short filamentose; gynophore slender, about 3.5 cm. long; ovary ovoid, white-velutinous.

Type in the U.S. National Herbarium, No. 1803911, collected near Unduavi, Department of La Paz, Province of Nor Yungas, Bolivia, at an altitude of 3,000 m., in forest along roadside, on Apr. 15, 1939, by W. J. Eyerdam (Goodspeed Expedition No. 25379). Duplicates at University of California and Chicago Natural History Museum.

This species belongs to the subgenus *Granadillastrum* and because of its laciniate-fimbriate bracts and general flower structure is evidently nearest *P. weberbaueri* and *P. trisecta*. Both of these have trifoliate leaves. The indument and general shape of the foliage are suggestive of *P. peduncularis*.

189. *Passiflora racemosa* Brot.

In describing the bracts of this species I said in the monograph: "bracts setaceous (?), soon deciduous." This statement is in error. In *Chase* 10125, which was cited, bracts are present, and Masters' plate in the *Flora Brasiliensis* shows a bract. They are ovate, about 1 cm. long and 8 mm. wide, tapering slightly at the base, thin-membranous, and pink, and are borne close to the base of the flower.

P. G. Greenway has recently sent me for study a superb lot of passionflowers from the Herbarium of the East African Agricultural Research Station, Amani, Tanganyika, nearly all of which are from plants grown at the Station and are of New World origin. Among these, No. 5942, collected by Greenway, is *P. racemosa*. The flowers are borne singly in the axils of fully developed leaves and are not in a raceme or on long branches with much reduced leaves. This plant may be of hybrid origin, or perhaps in a natural state the flowers may sometimes be solitary.

200. *Passiflora seemannii* Griseb.

This species has a rather unusual range of distribution. At the time that my monograph was prepared, the species was known in its native state by several collections from Panama and from scattered localities in Colombia. The following additional collections have subsequently been received at the U.S. National Herbarium:

COLOMBIA: Cundinamarca: San Francisco, alt. 1,550-1,580 m., *García-Barriga* 11051. El Meta: Villavicencio, alt. about 500 m., *Killip* 34445, 35692; *Cuatrecasas* 4673.

VENEZUELA: Amazonas: Yavita, *L. Williams* 14000.

209. *Passiflora capparidifolia* Killip

Material from British Guiana and the Rio Branco of Brazil was cited as this species in my monograph. The species is now represented in the U.S. National Herbarium by the following Venezuelan collections:

Bolívar: Between Río Torono and Salto de Auraima, edge of forest along Río Paragua, alt. 275 m., *Killip* 37539. Selvas de galería del Río Uari, Gran Sabana, *Tamayo* 3154.

The first of these collections was in fine flower and the second one bore young fruit. The description in the monograph may be amplified thus:

Bracts distinct to the base, broadly ovate, up to 5 cm. long and 3 cm. wide; sepals greenish white without, red-brown within; petals deep pinkish red; outermost corona filaments about 1.2 cm. long, banded with blue and white in upper part, red and white in lower part, the second series three times longer, blue and white in the upper two-thirds, red and white in the lower third; young fruit ovoid, about twice as long as wide, finely pilose, obcordate, about 5 mm. long and 3.5 mm. wide, reticulate.

210. *Passiflora popenovii* Killip

At the time that my monograph was prepared the only specimens of this species available to me were from Ecuador. The species was also collected in 1938 at El Tambo, Department of Cauca, Colombia, alt. 1,700 m. by K. von Sneidern (No. 1444), and was deposited in the Riksmuseet, Stockholm, and in the U.S. National Herbarium.

211a. *Passiflora brevifila* Killip, sp. nov.

PLATE 9

Frutex scandens omnino glaber, caule subquinqueangulato; stipulae anguste lineares subfalcatae; folia subcoriacea integra lanceolata vel oblongo-lanceolata acuminata basi rotundata; bractae liberae lanceolatae minute cuspidatae integrae basi subtruncatae, petiolo prope apicem 4–6 glanduloso; calycis tubus campanulatus, sepalis petalisque similibus oblongis obtusis; corona filamentis uniseriatis liguliformibus ad apicem leviter dilatatis; operculum fimbriatum filamentis rigidulis ad basim paulo incrassatis.

Woody vine, glabrous throughout; stem subquincangular; stipules narrowly linear, 5–6 mm. long, about 0.8 mm. wide, subfalcate, coriaceous; petioles 1–2 cm. long, bearing 4–6 minute glands near the apex, the glands short-stipitate or nearly sessile; leaves lanceolate or oblong-lanceolate, 12–14 cm. long, 5–5.5 cm. wide, acuminate, rounded at base, entire, penninerved (principal lateral nerves 6 or 7 to a side, arcuate-ascending), conspicuously reticulate beneath, subcoriaceous, concolorous, lustrous beneath; peduncles solitary, 2.5–3 cm. long, bracts free to base, lanceolate, 5–7 cm. long, 2–3 cm. wide, acuminate, minutely cuspidate, subtruncate at base, entire, similar in texture to the leaves; flowers about 6.5 cm. wide; calyx tube campanulate; sepals and petals similar, oblong, about 2.5 cm. long and 9 mm. wide, obtuse, apparently white; corona filaments in a single series, narrowly liguliform, slightly thickened at apex, 1 cm. long; operculum

a fringe of rather stiff filaments about 3 mm. long, slightly thickened at base; limen a thick ridge close to the operculum; floor of calyx tube smooth; ovary ovoid, green; fruit globose, about 6 cm. in diameter, the exocarp brittle, orange; seeds obovate, strongly flattened, 9–10 mm. long, 5 mm. wide, coarsely reticulate, tridentate at the apex, the middle tooth the more prominent.

Type in the U.S. National Herbarium, No. 1643741, collected at Vara Blanca de Sarapiquí, north slope of Central Cordillera, between Poás and Barba Volcanoes, Costa Rica, at an altitude of 1,890 m., in February 1938, by A. F. Skutch (No. 3591).

This species belongs to the subgenus *Granadilla* series *Laurifoliae*, where it is the only one with a single-ranked corona. The other representative of the series in Central America, *P. ambigua*, not only has a 5-ranked corona but the ovary is densely brown-tomentose. Doubtless the closest relative is *P. nigradenia*, of Bolivia, in which the corona is 2-ranked and the ovary finely sericeous.

213a. *Passiflora killipiana* Cuatr., sp. nov.

PLATE 10

Planta breviter hirtella vel pubescens, pilis patulis rufescentibus; stipulae lineari-subulatae; folia tenuiter subcoriacea ovato-oblonga vel elliptico-oblonga basi subrotundata apice acute acuminata margine remote minuteque crenulata, penninervia, nervis utrinque ferrugineo-hirtellis vel tomentulosis, venulis reticulatis utrinque prominulis, petiolo brevi subapicem biglanduloso; bractae liberae obovato-oblongae apice rotundatae sursum profunde dentatae; calycis tubus campanulatus, sepalis oblongis subapicem corniculatis, petalis brevioribus; corona filamentis 6–7 seriatis exterioribus liguliformibus valde longis, interioribus mediocribus, intermediis brevibus; operculum membranaceum profunde fimbriatum; ovarium velutino-tomentosum.

Plant hirtellous or pubescent nearly throughout, the hairs reddish, short, spreading; stem terete, slightly striate; stipules linear-subulate, 10–13 mm. long, 1 mm. wide, ferruginous-hirtellous, soon deciduous; petioles 7–11 mm. long, stout, ferrugineo-tomentellous, biglandular below the apex; blades 9–16 cm. long, 4.5–7.5 cm. broad, thin-subcoriaceous, ovate-oblong or elliptic-oblong, rounded or obtuse at base, acutely acuminate at apex, the margin subentire, minutely and distantly crenulate, hirtellous on the nerves above, more densely ferruginous-hirtellous on the nerves and the surface puberulous beneath, the midrib very prominent beneath, the secondary nerves 8–9 pairs, prominent, ascending, the smaller veins reticulate-prominulous on both sides; flowers 8–9 cm. wide, solitary, axillary; peduncles 3–4 cm. long, ferruginous-tomentellous, moderately thick; bracts thick obovate-oblong subrounded at apex, cuneate at base, coarsely and deeply toothed on the upper half, densely ferruginous-pubescent, 4.5–5.5 cm. long, 2–3 cm. broad; calyx tube cylindric-campanulate,

7–8 mm. high; sepals membranaceous, pubescent, 3.5–4 cm. long, 1–1.2 cm. wide, oblong, narrowed toward the obtuse apex, dorsally corniculate, the horn about 5 mm. long; petals smaller, thinner, oblong, about 3 cm. long, 0.5 cm. wide; corona filaments transversely colored-banded, in 6–7 series, the outermost narrowly ligulate, about 3 cm. long, 0.8 mm. wide, the innermost ligulate, about 6 mm. long, those of the intermediate series slender, 1.5–2.5 mm. long; operculum membranaceous, horizontal, the margin broadly recurved and deeply lacinate; limen cupular close to the gynophore; ovary ovoid-oblong, densely velutino-tomentose; gynophore about 1.5 cm. long.

Type in the U.S. National Herbarium No. 1952839, collected in the vicinity of La Pedrera near Río Caquetá, Comisaría del Caquetá, Colombia, in April 1944, by Richard Evans Schultes (No. 5875).

P. killipiana is closely related to *P. laurifolia* L., but differs from it and from the other known species of the section *Laurifolia* by the rufous or ferruginous, spreading pubescence or tomentum which covers several parts of the plant; *P. killipiana* differs also in the minute crenature of the leaves and in the thick, toothed bracts. The size of the different parts of the flowers and bracts and the relative length of the filaments of the several rows of the corona also distinguish this species from *P. laurifolia* and other related species.

The type of this species was examined by Killip in 1951 and classified as a new species in the section *Laurifolia*, but neither description nor name were given. The describer takes this opportunity to honor the man who did the largest and best work in *Passiflora* by naming the new species after him.

216. *Passiflora riparia* Mast.

Only material from Peru and Brazil was cited in my monograph. The following specimens from other countries are now in the U.S. National Herbarium:

BRITISH GUIANA: Western extremity of Kanuku Mountains, in drainage of Takutu River, alt. 500 m., *A. C. Smith* 3157.

COLOMBIA: Vaupes: Vicinity of Mitú, *Allen* 3340. Near Miraflores, alt. 300 m., *Gutiérrez & Schultes* 754 (Med). Putumayo: Mocoa, *Schultes & E. Smith* 2000.

Some specimens recently seen by me have the flowers borne singly in the leaf axils and not clustered on short, axillary branches as is typical of the species.

221a. *Passiflora pachyantha* Killip, *Lloydia* 2:198. 1939.

This species was based upon a specimen collected by A. C. Smith (No. 3620) on Mount Iramaikpang, in the northwestern portion of the Kanuku Mountains, British Guiana. The species belongs to a new section of the subgenus *Granadilla*, which comes between series 5, *Laurifoliae*, and series 6, *Serratifoliae*.

232. *Passiflora incarnata* L.

In the monograph I gave as the distribution of this species: "Virginia to Missouri, south to Florida and Texas; also in Bermuda. Introduced farther north in the United States" I also listed representative specimens of each state from which I had seen specimens.

Charles C. Deam wrote me that he found *P. incarnata* in 1899 on a hill near Wyandotte Cave, Crawford County, Indiana, and collected it on a bluff of the Ohio River, a half mile above Tell City, Perry County, Indiana. In his most useful Flora of Indiana (1940), he recorded it from two additional counties—all these localities being in the southern part of the State.

F. C. Gates likewise advised me that there are two specimens in the Kansas State College Herbarium from Labette County and Cherokee County, Kansas, collected in 1892 by A. S. Hitchcock.

No specimens were listed from these two States in my monograph. The distribution of this species should therefore be given as Virginia to southern Illinois and southeast Kansas, south to Florida and Texas.

245a. *Passiflora danielii* Killip sp. nov.

PLATE 11

Herba scandens, caule teneri glabro; folia subcoriacea ovato-lanceolata subabrupte acuminata integra basi leviter cordata subtus breviter adpresseque pilosa, petiolo glabro 2 paribus glandulis praedito; calycis tubus late campanulatus, sepalis lineari-lanceolatis, petalis sepalis similibus obtusis; corona filamentis circa 5-seriatis in duobus exterioribus seriebus subcapillaribus ceteris filiformibus minuteque capitellatis; operculum membranaceum erectum ad medium fimbriatum; ovarium glabrum.

Herbaceous vine; stem terete, slender, striate, glabrous; stipules semicordate, 1.5–2 cm. long, 6–9 cm. wide, abruptly cuspidate-acuminate, attached laterally slightly above the rounded base, the costa strongly eccentric; petioles 2.5–4 cm. long, glabrous, bearing slightly above the middle a pair of sessile, laterally compressed, concave glands about 1.5 mm. long and wide and another pair at the apex, the latter pair sometimes being borne instead at the margin of the blade close to the petiole; leaf-blades ovate-lanceolate, 10–12 cm. long, 6–6.5 cm. wide, subabruptly acuminate, slightly cordulate at the base, entire, 7-nerved, closely reticulate, subcoriaceous, concolorous, sublustrous and glabrous above, short-pilose on the nerves and veins beneath, the hairs divaricate, closely appressed to the surface of the blade; peduncles solitary, terete, 8–9 cm. long, slender, glabrous, articulate about 5 mm. below the apex; bracts unknown; calyx tube broadly campanulate, about 6 mm. long, 8–9 mm. in diameter at the throat, introrse at the base; sepals linear-lanceolate, 2–2.2 cm. long, about 8 mm. wide at the base, horned dorsally just below the apex,

the horn 1.2–1.3 cm. long; petals similar to the sepals about 1.3 cm. long and 5 mm. wide, obtuse; corona filaments apparently in about 5 series, the 2 outer filiform, almost capillary, 1.5–2 cm. long, those of the succeeding series filiform, about 3 mm. long, minutely capitate; operculum membranous, erect, about 5 mm. long, filamentose to the middle; nectar ring a low ridge; limen tubular, 4 mm. high, closely surrounding the base of the gynophore; ovary ovoid, glabrous.

Type in the U.S. National Herbarium, No. 1742750, collected at Cocorná, Department of Antioquia, Colombia, in August 1938, by Brother Daniel (No. 1536).

This species belongs to the series *Simplicifoliae* of the subgenus *Granadilla* (species 245–258 of my monograph). The unusual petiolar glands, which are more like the auricular appendages in *P. auriculata*, at once distinguish it from the other species of this series, nearly all of which have filiform glands. The slender peduncles, which are much slenderer than the stem, separate it from the four species of the first group within this series, and the long peduncles distinguish it from the other *Simplicifoliae*. The large, conspicuous horns are duplicated among species of this series only in *P. praeacuta*.

266. *Passiflora picturata* Ker

This rare species, whose distribution was recorded as "Surinam to Pará, Brazil" in my monograph, was also collected by the eminent Colombian botanist, Lorenzo Uribe Uribe, in eastern Colombia. The specimen in the U.S. National Herbarium bears the following data:

COLOMBIA: Meta: Acacías, near the Río Acacías, alt. 450 m., July 29, 1946, *Uribe Uribe* 1334. Flowers purple.

287. *Passiflora menispermifolia* H.B.K.

An extreme variant of this species has been collected in Bolivia by W. J. Eyerdam (Goodspeed Expedition 24718). It was found on the new road to Todos Santos, 130 km. northeast of Cochabamba, north side of Río San Mateo, near Chimore, Province of Chaparé, Department of Cochabamba, at an altitude of 700 m., hanging from bushes in a damp thicket. The flowers are noted as cerulean blue. Here also belongs *Buchtien* 4652, collected from Antahuacana, Department of Espíritu Santo, at an altitude of 750 m., which, in the monograph of Passifloraceae, I referred with some doubt to *P. rojasii* Hassl.

In this Bolivian variant, the leaves are scarcely lobed, are more acute, and are of a thinner texture.

309. *Passiflora pittieri* Mast.

This species has been known only from the type material collected at Santo Domingo, Golfo Dulce, Costa Rica. Additional collections in the U.S. National Herbarium may now be listed as follows:

PANAMA: Isla de Coiba, March 1938, *Méndez* 140. Forests around Pinogana, Darién, *Pittier* 6964.

COLOMBIA: Antioquia: Forest at Guapá, 53 km. south of Turbo, April 25, 1945, *Haught* 4600. Forest near Chigorodo, 40 km. south of Turbo, *Haught* 4695.

This record is one of several of species of the Costa Rican lowlands occurring in the Darién region of Panama and extending into northwestern Colombia.

Pittier 6964 consists of a few flowers only, and I did not discuss the collection in my monograph.

The leaves of the Méndez and Haught specimens are oblong or oblong-lanceolate, rather than prevailing obovate as in the type, and are proportionately narrower. The largest one is 19 cm. long and 6.5 cm. wide.

309a. *Passiflora cardonae* Killip, Brittonia 3:172. 1939.

An additional collection was made at:

VENEZUELA: Bolívar: Cerro de Auyantepui, December 1937, *Cardona* 284 (VEN).

348. *Passiflora longiracemosa* Ducke

Known heretofore only from British Guiana and northern Brazil, this species has been collected in the forest at Salto de Pará, middle Caura River, State of Bolívar, Venezuela, by Llewelyn Williams (No. 11369). Though the leaves of this species are variable, I have seen none heretofore of the shape of those recently collected. They are broadly ovate-lanceolate, tapering gradually to a blunt tip, and are about 15 cm. long by 9 cm. wide.

349. *Passiflora securiclata* Mast.

The intensive exploration that has taken place in the Orinoco Basin in the last 10 years has led to the collection of much additional material of this species. I cited in my monograph only six specimens from Venezuela and none from Colombia. The numerous specimens now available show a greater variation in the shape and texture of the leaves. The description of the apex of the leaves as given in my monograph reads, "obtuse, usually emarginate, rarely bluntly short-acuminate." Masters, in the original account of the species, used the term "acute," though some of the leaves on the type specimen are rounded or almost truncate at the apex. Several recent specimens have leaves which are oblong-lanceolate or even lanceolate, tapering

to an acute apex. In many of them there is a dark band about the margin of the leaves. The texture varies from thick-coriaceous to almost membranous. No differences are discernible in the flowers, and it does not seem desirable to propose any segregates.

The additional material now in the U.S. National Herbarium consists of the following collections:

VENEZUELA: Anzoátegui: Río Chive, *Pittier* 15023. Bolívar: Medio Río Caura, *Williams* 11618, 11716. Río Paragua, *Cardona* 746; *Killip* 37534. Amazonas: Puerto Ayacucho, *Williams* 13125. San Antonio, Río Orinoco, *Williams* 15069. Tamatama, *Williams* 15245. Esmeralda, *Williams* 15310, 15515.

COLOMBIA: Arauca: Matabubosa, Río Meta, *Cuatrecasas* 4237. Boyacá: Río Guachiria, *Haught* 2663. Vichada: Curazao, Río Meta, *Cuatrecasas* 4134.

Two of these specimens, *Pittier* 15023 and *Williams* 15069, bear mature fruit, which, apparently not hitherto known, may be described thus:

Fruit ovoid, about 4.5 cm. long, and 3 cm. wide; the pericarp glabrous, brittle, yellowish; seeds obovate, 5–6 mm. long, 4–4.5 mm. wide, flattened, reticulate.

“Parcha” is given as the local name for several of the specimens.

352. *Passiflora pyrrhantha* Harms

Recent collections made are:

COLOMBIA: Meta: Monte de Machadero, Ocóa, near Villavicencio, *Hermann* 11120. Sierra de la Macarena, *Philipson*, *Idrobo*, & *Jaramillo* 2225.

PERU: Loreto: Gamitanacocha, Río Mazán, *J. M. Schuncke* 358.

353. *Passiflora spinosa* (Poepp. & Endl.) Mast.

Fruiting material of this species has been collected for apparently the first time by Cuatrecasas (No. 6846) at Mitú, Vaupés, Colombia. The fruit may be described thus:

Fruit ovoid, about 5 cm. long, and 2.5 cm. in diameter, subhexagonal, very minutely pilose, ochre; seeds broadly obovate, 7 mm. long, 5 mm. wide, strongly compressed, coarsely reticulate. The specimen is in the Herbario Nacional Colombiano.

3. *Mitostemma brevifilis* Gontsch.

An additional collection was made at Estacas, Campo Grande, Mato Grosso, Brazil, on Sept. 10, 1936, by Archer & Gehrt (No. 170). This species is known otherwise only from the type material collected on the Rio Pardo, Rio Grande do Sul (*Riedel* 535).

4. *Dilkea acuminata* Mast.

An additional collection was made by Philipson and Idrobo (No. 1820) at Central Mountains, Sierra de la Macarena, Meta, Colombia, at an altitude of 8,000 m., on Dec. 20, 1949 (BM). “Climber; fruit

yellow" are the notations given. This species is otherwise known only from the type specimen collected at Manáos, State of Amazonas, Brazil.

List of Exsiccatae

The numbers in parentheses refer to the species number in the text.

- | | |
|---|--|
| Allen 3340 (216). | Méndez 108 (309). |
| André 3478 (69a). | Metcalf (Goodspeed) 30784 (162). |
| Archer & Gehrt 170 (Mitostemma
brevifilis). | Mexía 7645 (69). |
| Balls 7360 (69a). | Mille s.n. in 1918 (69). |
| Buchtien 4652 (287). | Mille 222 (69). |
| Burke, David, 184 (148b). | Ochoa 1565 (69). |
| Cárdenas 3886 (173). | Penland & Summers 1006 (173). |
| Cardona 284 (309a); 746 (349). | Pérez-Arbeláez 669 (100). |
| Chase 10125 (189). | Pérez-Arbeláez & Cuatrecasas 8083
(154a). |
| Cuatrecasas 4134 (349); 4237 (349);
4673 (200); 5136 (147); 6846 (353);
9479 (148a); 10776 (100); 11886 (14a);
13538 (148a); 20935 (69). | Philipson & Idrobo 1820 (Dilkea
acuminata). |
| Daniel 1536 (245a); 1916 (177). | Philipson, Idrobo, & Jaramillo 2225
(352). |
| Davidson, M. E., 336 (61). | Pittier 6964 (309); 15023 (349). |
| Ducke 34968 (330a). | Raimondi 7807 (155a); 8241 (155a). |
| Espinosa 617 (135); 621 (135); 806
(135); E965 (166A); 1314 (135). | Riedel 535 (Mitostemma brevifilis). |
| Ewan 15899 (69a). | Schultes 5875 (213a). |
| Eyerdam (Goodspeed) 24718 (287);
25379 (180a). | Schultes & E. Smith 2000 (216). |
| Firmín 310 (69). | Schultes & Villarreal 7417 (69a). |
| Funck & Schlim 1381 (137). | Schuncke 358 (352). |
| García-Barriga 7757A (69a); 7785A
(69); 11051 (200). | Skutch 3591 (211a). |
| Greenway 5942 (189). | Smith, A. C., 3157 (216); 3620 (221a). |
| Gutiérrez & Barkley 18C294 (170). | Sneidern, von, 1442 (177); 1444 (210). |
| Gutiérrez & Schultes 754 (216). | Stevens 258 (69). |
| Haught 2663 (349); 4600 (309); 4695
(309). | Steyermark 31281 (46a); 31519 (46a);
32884 (26); 32985 (46a); 46761 (26);
52879 (10); 52932 (4); 54397 (138);
54493 (159a); 56503 (149); 57240
(111); 57277 (137). |
| Hermann 11120 (352). | Tamayo 3025 (10); 3154 (209). |
| Humboldt & Bonpland (69). | Uribe Uribe 1061 (148a); 1334 (266). |
| Killip 34445 (200); 35692 (200); 37534
(349); 37539 (209). | Wedel, H. von, 2120 (61); 2421 (4). |
| Killip & García 33482 (63). | Williams, L., 11369 (348); 11618 (349);
11716 (349); 13125 (349); 14000 (200);
15069 (349); 15245 (349); 15310 (349);
15515 (349). |
| Lehmann 675 (69); 8020 (69). | |
| Matuda 1892 (26). | |



UNITED STATES NATIONAL MUSEUM

HERBARIO NACIONAL COLOMBIANO

Passiflora ursina Killip
et Cuatrecasas.

Holotypus

COLOMBIA, DEPT. BOGOTÁ, MUNICIPIO DE BOGOTÁ, CERRILLO DE LA NEBLINA, 2900-3100 m., 1940.

LOCALITY: CUATRECASAS

PASSIFLORA URSINA KILLIP & CUATRECASAS



PASSIFLORA CUATRECASASII KILLIP



FLORA OF Colombia, No. 184
Passiflora ...
...
...
...
David Burke (det.)

PASSIFLORA RIGIDIFOLIA KILLIP



PASSIFLORA BOYACANA KILLIP

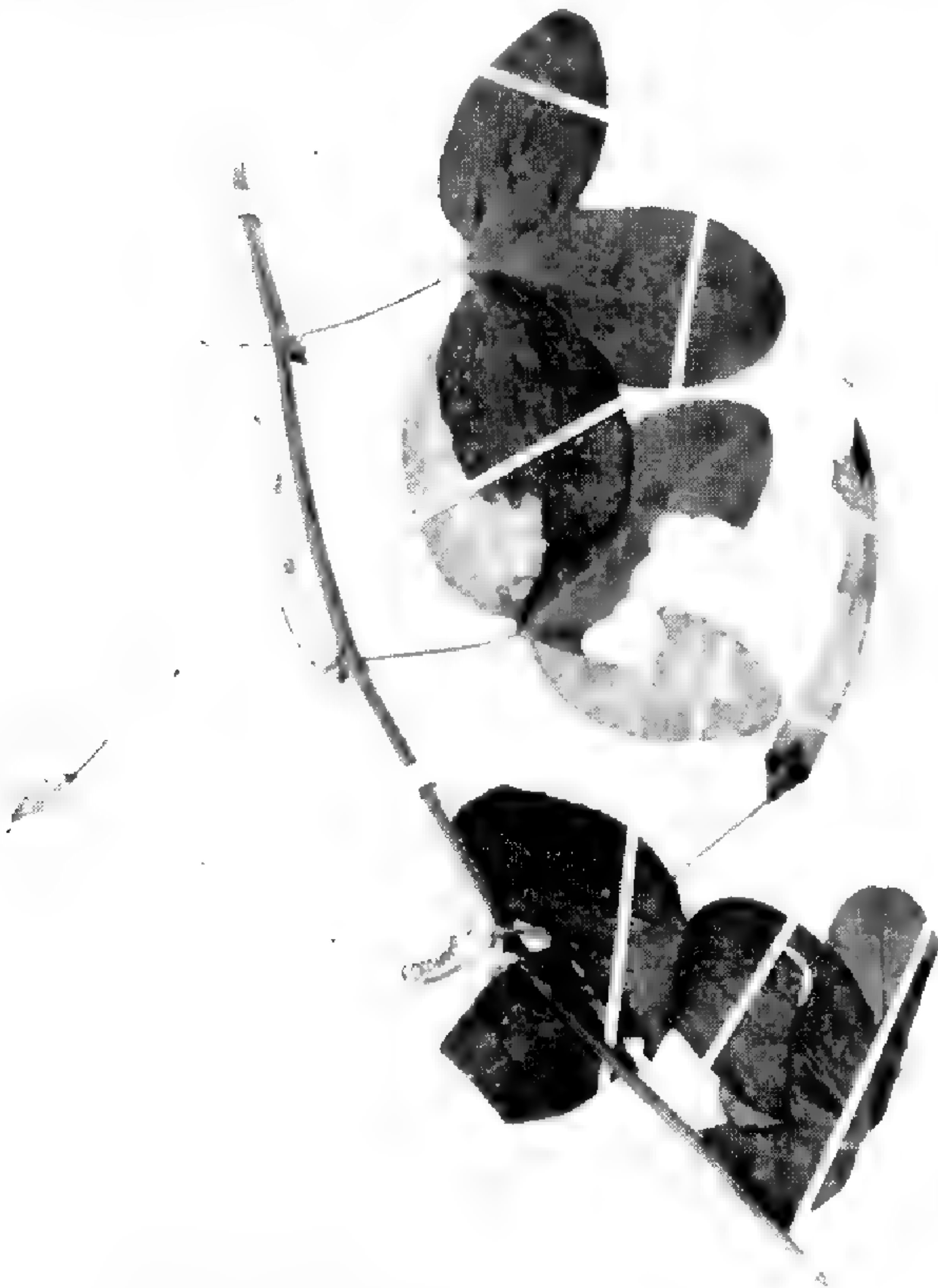
Museo de Historia Natural de la Universidad de Lima

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Director Fundador: Dr. Carlos Rospigliosi Vigil

Herbario Raymondi



A. Raimondi, Herbario in Peruvinum

Procedencia.....*Chorrillos-Cajamarca* | Familia ... *Passifloraceæ*
Nom. Vulg..... | Género y Especie...*Passiflora*...

PASSIFLORA RAIMONDII KILLIP



CHICAGO
HARVARD MUSEUM

54493 PLANTS OF ECUADOR

Passiflora

"fullan"

Petals deep salmon-rose, the midrib
with pale green center

PASSIFLORA ZAMORANA KILLIP



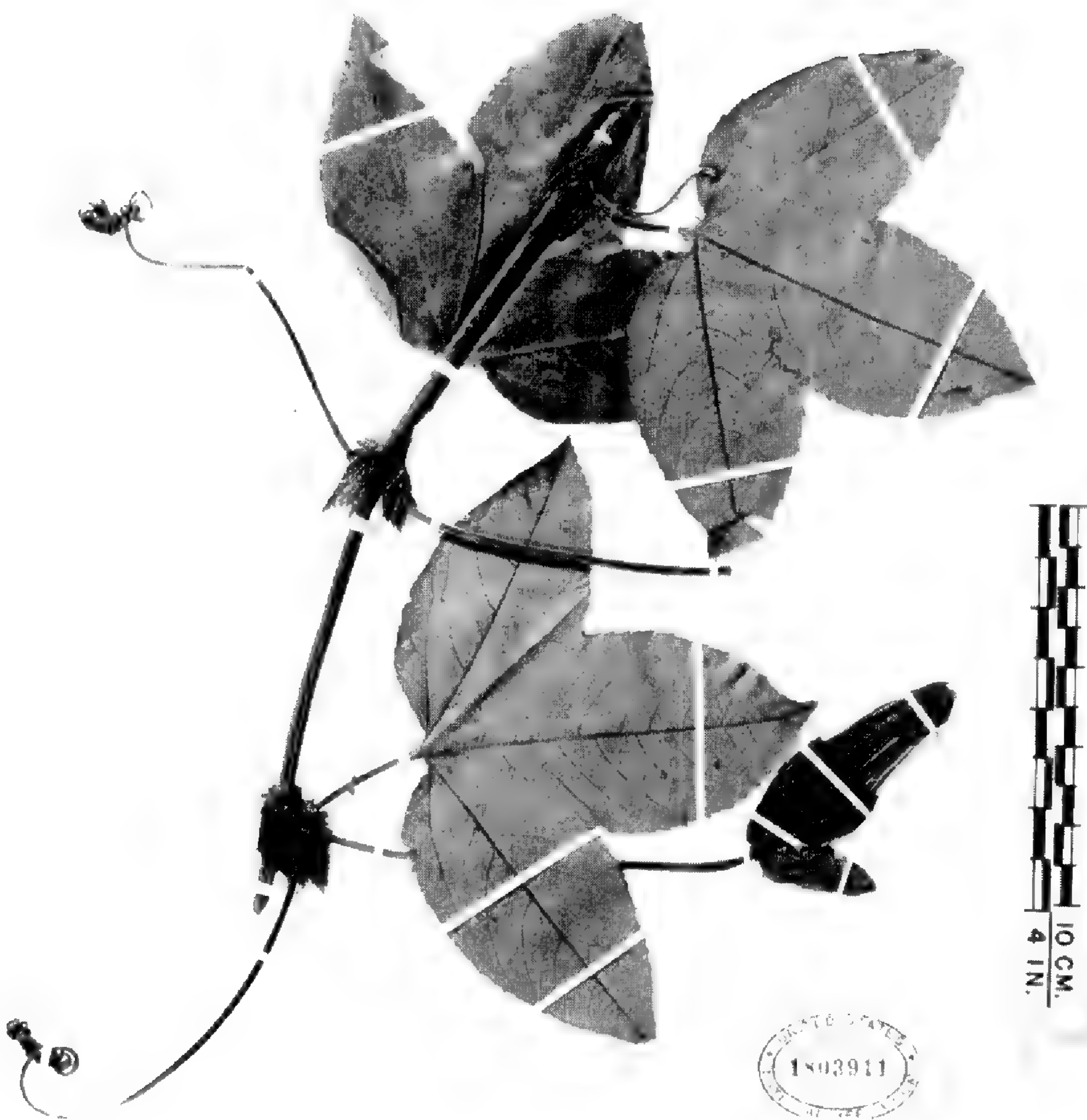
Passiflora loxensis Killip & Cuatr.
Holotype
HERBARIUM UNIVERSITATIS LOXENSIS

N. E. 966

Passifloraceae
Passiflora

Flor grande (17 cm. longitud) color lila azulado.
Culmina en ...
Hort. ... 3000 m alt.
Dr. R. ... Equinox

PASSIFLORA LOXENSIS KILLIP & CUATRECASAS



UNITED STATES NATIONAL MUSEUM

UNIVERSITY OF CALIFORNIA
Herod Botanical Garden Expedition to the Andes, 1928-30
Director T. H. Gentry

Passiflora macropoda Killip
sp. n.

PASSIFLORA MACROPODA KILLIP



UNITED STATES NATIONAL MUSEUM

PLANTS OF COSTA RICA

Passiflora brevifila Killip
type

PASSIFLORA BREVIFILA KILLIP

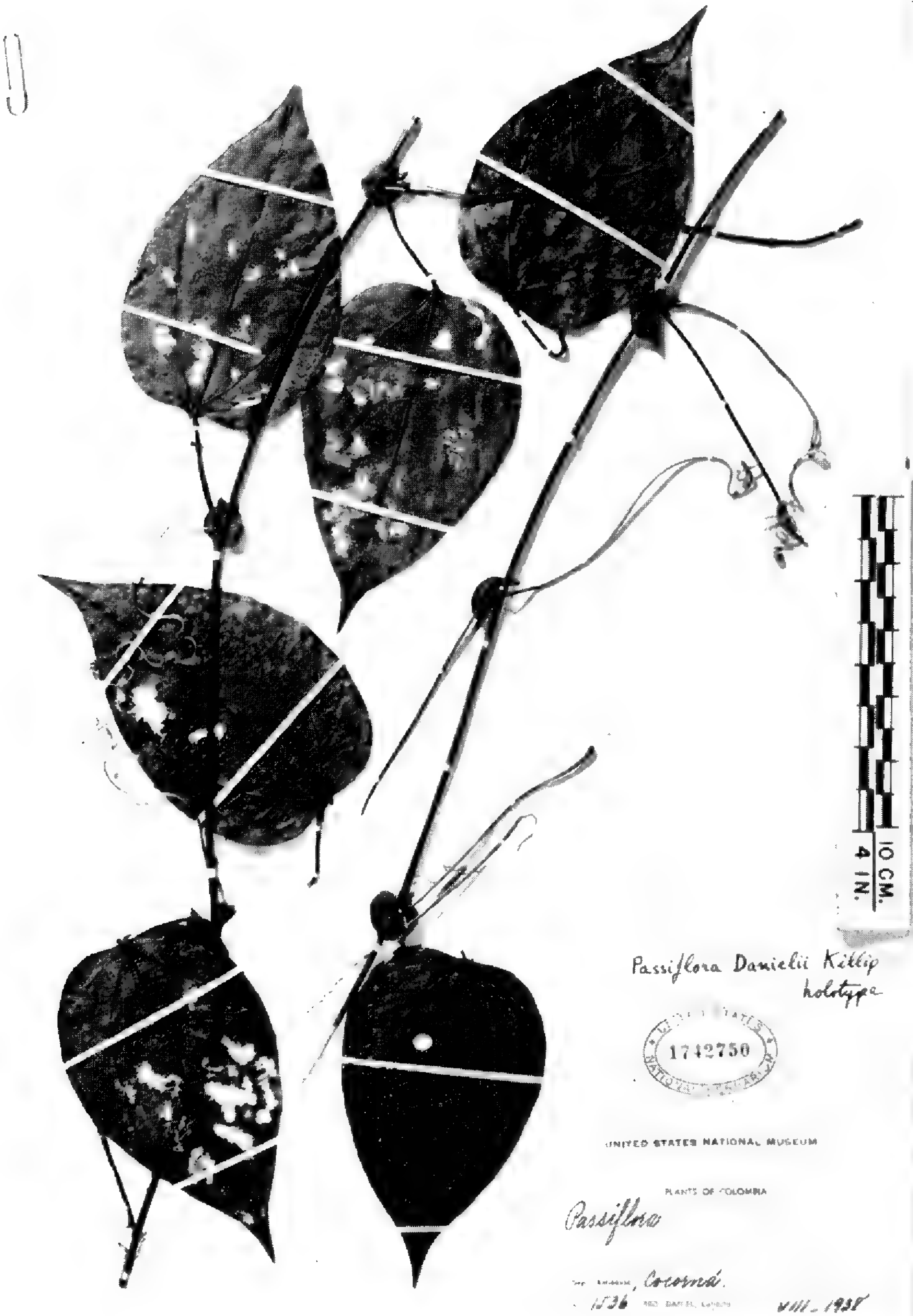


PLANTAE COLOMBIANAE
CAQUETA

UNITED STATES NATIONAL MUSEUM

PLANTAE COLOMBIANAE
CAQUETA

PASSIFLORA KILLIPIANA CUATRECASAS



PASSIFLORA DANIELII KILLIP

U N I T E D S T A T E S N A T I O N A L M U S E U M

CONTRIBUTIONS FROM THE UNITED STATES NATIONAL HERBARIUM

VOLUME 35, PART 2

A TAXONOMIC REVISION OF THE
HUMIRIACEAE

By JOSE CUATRECASAS



BULLETIN OF THE UNITED STATES NATIONAL MUSEUM

SMITHSONIAN INSTITUTION • WASHINGTON, D.C. • 1961

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A TAXONOMIC REVISION OF THE HUMIRIACEAE

JOSE CUATRECASAS

Introduction

My special interest in the tropical trees and shrubs of the family Humiriaceae developed many years ago while I was studying my own collections, gathered on expeditions sponsored by the regional Government of El Valle del Cauca, from the Pacific coast of Colombia. What drew my attention most were the rare fruit collected and their similarity to the fossil specimens of *Sacoglottis cipaconensis* presented to me some years earlier in Bogota by the geologist J. Royo Gómez. These fossils proved to belong to the genus *Vantanea* rather than to *Sacoglottis*. Notwithstanding the exceptionally good work of Urban in the "Flora Brasiliensis," the existing literature lacked information on the structure of the fruit, information indispensable to a more complete taxonomic understanding of the family. In view of the collections made since Martius' gigantic work on neotropical botany, some revision of the group seemed necessary. In 1951, while in Chicago, I initiated this revision with the cooperation of T. Just, who intended to prepare a section on paleobotany in the planned synopsis; however, the project was discontinued. In 1957, with the primary purpose of writing the Humiriaceae for the "Flora of Colombia," I started anew with a taxonomic revision of the entire family; the results of this study are summarized in the present publication.

For this revision I have used the large collections of the U.S. National Museum, in the U.S. National Herbarium (US), which have recently been augmented by the collections formerly in the National Arboretum. I have also used those of the:

New York Botanical Garden, New York (NY),
Gray Herbarium, Harvard University, Cambridge, Massachusetts (GH),
Arnold Arboretum, Harvard University, Cambridge, Massachusetts (A),
School of Forestry, Yale University, New Haven, Connecticut (Y),
Museum d'Histoire Naturelle, Paris (P),
Royal Botanic Gardens, Kew, Surrey (K),
British Museum (Natural History), London (BM),
Naturhistoriska Museum, Stockholm (S),
Botanische Staatssammlung, Munich (M),
Botanical Museum and Herbarium, Utrecht (U),
Museu Goeldi de Historia Natural, Belém do Pará (MG),
Instituto Agronomico do Norte, Belém do Pará (IAN), and
Instituto de Ciencias Naturales, Bogotá (COL).

The above-mentioned herbaria have the largest existing collections of members of Humiriaceae, and their examination has resulted in a considerably greater understanding of the family than we had previously. These herbaria combined have a copious representation of the important historical collections made by Schomburgk, Spruce, Martius, and others, as well as of more recent collections, among them those of Ducke, Maguire, and the Boschwezen (Forest Service) of Surinam. Nearly all types or isotypes of the described species are found among the material of the herbaria mentioned. The amount of fruiting material in the modern collections, though not abundant, is sufficient to allow us to draw new lines in the concept of the family and its genera. Especially rewarding have been the amazing Brazilian collections of Adolfo Ducke. The relative importance of the collections used can be readily seen by examining the index of collectors at the end of this paper (p. 187).

The present revision is based on the classical method of comparative morphology. I utilize the fruit structure to a considerably greater extent than previous authors. The paper concludes that the *Humiriaceae* are to be maintained as an independent family with 8 genera, 49 species, and many subspecies, varieties, and forms.

The introduction to this paper begins with a historical sketch of contributions to our knowledge of the family and a discussion of the phenomena of drift fruit and fossils. There follows, because of its taxonomic importance, a discussion of the structure of the fruit and also a discussion of taxonomic relationships and evolutionary trends. No data on the cytological structure of any Humiriaceae are available. The considerations of evolutionary trends are founded on comparative gross morphology and are merely tentative. The paleontologic data are limited to the mention of published species and to a few taxonomic suggestions.

The main part of the paper is devoted to classification and taxonomic descriptions of the family and the tribes, genera, species, subspecies, varieties, and forms comprising the family. Included are plates and figures comparing and contrasting related forms. The plates are grouped following p. 84. The figures appear in the text near the species to which they refer.

The citations of collections constitute an important part in a monographic work and, because of the relative scarcity of locality data, I consider it useful to publish the information given on the herbarium labels by each collector. For greater accuracy these data appear in their original language. In the citations of herbaria where specimens are deposited, I use the abbreviations of Lanjouw's "Index herbariorum." In citing the photographic series of the Chicago Natural

History Museum, the abbreviation "Photo F.M." has been used preceding the number.

I wish to extend my thanks to the directors and curators of the herbaria who have aided by lending me collections or giving me facilities for my work, among them especially Albert C. Smith, Director of the Museum of Natural History of the U.S. National Museum; Jason R. Swallen, head curator of Botany; Lyman B. Smith, curator of phanerogams, who has checked the manuscript; Roland Brown, honorary curator of paleobotany, who has been of great help locating humiriaceous fossil collections; the artist Russell Zimmermann, who made all but four of the figures with a complete understanding of my interpretations; and Paula Gerard and Jane Roller, who made the accurate drawings of figure 1.

The work for this revision has been carried out at the Department of Botany of the U.S. National Museum, with the help of a grant from the National Science Foundation.

HISTORICAL SKETCH

1775: Aublet publishes in his "Histoire des plantes de la Guiane française" the first descriptions and drawings of Humiriaceae—*Houmiri balsamifera* and *Vantanea guianensis*—two new genera and species named after the Caribbean names "Houmiri" and "Iouantan." The first genus is characterized by small flowers with 20 stamens and the second by large flowers and many stamens. He places the genera in the class Polyandria and the order Monogynia of Linné's sexual system.

1777: Scopoli, like other botanists of the time, finding the names given by Aublet barbarous, proposes "Wernisekia" for "Houmiri" (Introd. Hist. Nat.).

1789: Schreber, for the same reason, in his eighth edition of "Linné's genera plantarum" changes "Houmiri" to "Myrodendrum" and "Vantanea" to "Lemniscia" and writes: "Aubletiano vero nomenclaturae quum nimis sit barbara, aliam quin substituerem, me continere nequivi." They are included in the Polyandria Monogynia.

1789: Jussieu, trying to Latinize Aublet's name, gives it the spelling "Houmiria," in his "Genera plantarum."

1792: Lamark publishes a new species from French Guiana—*Vantanea parviflora*.

1800: Willdenow, following Schreber, in his edition of Linnaeus' "Species plantarum" adopts "Lemniscia," thus correcting its spelling, and, for *Vantanea guianensis*, he uses "Lemniscia floribunda."

1805: St. Hilaire completes the "Latinization" initiated by Jussieu with the spelling "Humiria." He includes the plant in "Classe

Polyandrie" and "Ordre Monogynie" (Exposition des familles naturelles).

1824: Nees and Martius publish the new genus *Helleria*, based upon *H. obovata*, not noticing that it is congeneric with *Vantanea guianensis*. The authors place the genus next to *Humiria* and consider its close relationship to several groups, primarily *Aurantiae* and *Ternstroemiaceae*.

1827: Martius publishes (Nov. Gen. Sp. Pl. Br.) detailed descriptions of *Humirium crassifolium* and *H. floribundum*, and gives a new spelling to the generic name, "Humirium" (proposed in ms. by Richard). Martius describes the genus *Helleria* and a new genus, *Sacoglottis*, based upon *Sacoglottis amazonica*, and distinguished by 10 stamens. He includes *Sacoglottis* in Linnaeus' Monadelphia-Decandria, whereas he places *Humirium* and *Helleria* in Monadelphia-Polyandria. Martius comments on the close relationship between the three genera and traces their differences with the genera considered related to *Meliaceae*, *Symplocaceae*, and *Styracaceae*.

1829: Jussieu gives, in St. Hilaire's "Flora Brasiliae meridionalis," for the first time a taxonomic category (order=family) to these three genera under the name "Humiriaceae." He adds the new species *Humirium montanum*, *H. parvifolium*, and *Helleria ovalifolia* and lists *Helleria obovata* Nees. & Mart.

1830: Lindley (Introd. Nat. Syst. Bot.), considers the tribe Humiriaceae and their relation to the *Aurantiaceae*, *Diosmeae*, and *Rutaceae*.

1840: Endlicher in "Genera plantarum" lists this family as "Ordo CCXXII-Humiriaceae," following Jussieu and recalling Martius' considerations about the close relationship between the three genera with *Symplocaceae* and *Styracaceae*, and their separation from the *Meliaceae*.

1842: Casaretto publishes *Humirium dentatum*.

1843: Bentham publishes four new species of *Humirium* from the Guianas—*H. densiflorum*, *H. guianense*, *H. obovatum*, and *H. subcrenatum*.

1848: Planchon, in his studies "Sur la famille des Linées," makes comparisons between *Humirium* and *Erythroxylon*, and the *Linaceae*, and shows their close relationship; nevertheless, he considers the Humiriaceae independent but connected with the *Linaceae* through *Roucheria*. The main differential characters given are the thick connective of the anthers, the intrastaminal free disk, and the single style. Planchon's transverse division of the ovary cavities by false septa are only true of *Humiria*.

1850: Miquel publishes *Humirium surinamensis*.

1853: Bentham publishes "Notes on Humiriaceae," which is the first synthetic account of this family, and which defines with precision

and simplicity the "order" and its subdivisions. He identifies *Helleria* of Martius with *Vantanea*; supposedly Martius failed to recognize the latter genus because of inaccuracies in Aublet's drawings, which overlooked the enlarged connective of the anthers. Bentham distinguishes three genera by the number of stamens: *Vantanea* with numerous stamens (75–150); *Humirium* with 20 stamens, and *Sacoglottis* with 10 stamens. He does not consider the structure of the thecae of the anthers, but uses the number of ovules in the definition of the genera: *Vantanea* with two ovules in each cavity of the ovary; *Sacoglottis* with one; *Humirium* with both cases being true. Bentham lists 4 species of *Vantanea* (*guianensis*, *minor* sp. n., *obovata*, and *ovalifolia*), 12 species of *Humirium* (*crassifolium*, *guianense*, *floribundum*, *montanum*, *obovatum*, *cuspidatum* sp. n., *subcrenatum*, *dentatum*, *balsamiferum*, *macrophyllum* sp. n., *densiflorum*, and *oblongifolium* sp. n.), and 2 species of *Sacoglottis* (*amazonica* and *guianensis* sp. n.).

1860: Baillon, in *Adansonia*, discusses the family with the descriptions of three examples—*Sacoglottis amazonica*, *Humirium arenarium*, and *Helleria*—that he considers different from the Ericaceae and Styracaceae.

1862: Baillon describes a new genus based on a West African species, *Aubrya gabonensis*. He divides the Humiriaceae into two series: One with "free stamens" (*Vantanea* and *Aubrya*), and the other with monadelphous stamens. He distinguishes *Sacoglottis* with 10 stamens and uniovulate ovary cells from *Humirium* with 20 stamens and biovulate ovary cells.

1862: Bentham and Hooker define "Ordo XXXV Humiriaceae" mainly by small sepals, disk, stamens 10– ∞ , carnose connective, and solitary ovules or rarely 2 in each cell. They distinguish 3 genera according to the number of stamens and disk: *Vantanea*, numerous stamens; *Humiria*, 20 stamens monantheriferous and sometimes 5 stamens triantheriferous; and *Sacoglottis*, 10 stamens. Bentham considers this order closely related to the Linaceae series Ixonantheae but different from it because of the enlarged connective of the anthers.

1870: Schnizlein publishes *Humirium compactum*.

1873: Baillon, in *Adansonia*, sees no reason for replacing Aublet's name "Houmiri." He compares this form with the Erythroxylaceae, *Hebepetalum*, and *Ixonanthes* (Linaceae) and sees close affinities. *Vantanea parviflora*, which Richard (ms.) considered apart (*Vantaneoides*), has only strongly contorted corolla and imbricate calyx, features insufficient to separate it from *Vantanea* (*V. guianensis*, with tubulose calyx). Nor does he see a difference between *Helleria* and *Vantanea*. He writes that the ovary cells are alternipetalous as in *Hugonia*, *Hebepetalum*, and *Ixonanthes*, and that the ovules are pendulous with

the micropyle pointing upward, almost collateral or superposed, as in *Ixonanthes* and *Erythroxylon*. He considers only 1 genus in Humiriaceae, *Houmiri*, with 15 species distributed in 5 sections: *Houmiri* properly (*Humirium*), *Aubrya*, *Saccoglottis*, *Vantaneoides*, and *Vantanea*. All are included in the family Linaceae, series *Houmirieae* Baillon.

1874: Baillon, in "Histoire des plantes," describes as examples three types of Humiriaceae and reiterates his viewpoints already mentioned in *Adansonia*. He divides the genus *Houmiri* into sections: Sect. *Aubrya* with 10 free stamens; Sect. *Saccoglottis* with 10 stamens and 10 staminodia; Sect. *Humirium* with 20 stamens; Sect. *Vantanea* with 20–30–60 stamens; and Sect. *Vantaneoides* never formally published. They form the series *Houmiriées* in the Linaceae.

1877: Urban publishes a thorough treatment of the family in the "Flora Brasiliensis" of Martius. His detailed morphologic investigations on the structure of the thecae of the anthers, number of ovules in the ovary cells, position of the carpels, and number and structure of stamens are the greatest contribution to the systematics of the Humiriaceae. Urban finds in these characters the basis for a new concept of classification. He divides the family into two primary groups according to the number of cells in the thecae of the anthers. Thecae with two loculi and many stamens define *Vantanea*; unilocular thecae and fewer stamens (10–20) define *Humiria* and *Sacoglottis*. Urban distinguishes *Humiria* for having biovulate carpels opposite the petals from *Sacoglottis*, which has uniovulate carpels opposite the sepals. He further finds that the sacs of the anthers are glabrous in *Sacoglottis* and pilose in *Humiria*. Contrary to previous authors (Planchon, Baillon, and Bentham), Urban finds that the number of stamens is not the differential character between *Humiria* and *Sacoglottis*; *Humiria* has 20 stamens, but *Sacoglottis* also includes species with 20 stamens. Going further in the systematization and considering the number of stamens and anthers also important, Urban divides *Sacoglottis* into three subgenera: I, *Humiriastrum*, with 20 undivided stamens, 3 species; II, *Schistostemon*, with 20 stamens, the larger 5 tridentate bearing 3 anthers, 4 species; III, *Eusacoglottis*, with 10 stamens, 3 species. Urban's system proves to be definitive because later discoveries and studies reinforce the concepts and taxonomic trends devised by him. All later botanists follow his treatment. Unfortunately, Urban sees very few fruit and does not use them in his system. All 19 species that Urban treats are Guianan-Brazilian. Several new combinations, varieties, and one new species (*Sacoglottis dichotoma*) are described in the "Flora Brasiliensis."

1878–1893: Urban adds three new species of *Sacoglottis* and describes the fruit of a *Sacoglottis* sent to him by Schwacke and Glaziou. In

these globose, large fruit with hard endocarp filled with resinous cavities, Urban sees a new difference between *Sacoglottis* and *Humiria*, which confirms his separating the two genera on a basis other than the number of stamens. In this connection Urban writes the interesting following paragraph: "The fruit of Humiriaceae are very seldom in botanical museums. For the preparation of my monograph of the family, in 1877, I could only obtain fruit from *Humiria floribunda* and *Sacoglottis oblongifolia*. Afterward, I have seen fruit of a *Sacoglottis* species collected by Poeppig in the Amazonas, of a *Humiria* (or *Vantanea*?) from the same place (almost the size of a hen's egg), and another of a *Sacoglottis* species found floating on the shores of Jamaica (see Morris, in *Nature*, 1889, p. 322). Since no herbarium specimens of the fruit mentioned were available, it was not possible to identify the species. The identification of the genera could be solved only through the analogous structure of the fruit with those of *Humiria floribunda* or *Sacoglottis oblongifolia*. Through the examination of the fruit it is very satisfactory to see confirmed my viewpoint on the separation of *Humiria* and *Sacoglottis*. The fruit were sent to me in dried condition by Schwacke and preserved in alcohol by Glaziou. My separation between *Humiria* and *Sacoglottis* was established on the basis of the position of the ovary cells and number of ovules (in contrast to the formerly prevailing criterion based on the number of stamens), so that the differences between the two genera, as I saw them, harmonize with differences in the structure of the fruit. The fruit of *Vantanea*, which up to now I have not seen, could possibly indicate that this genus is more closely related to *Humiria* than to *Sacoglottis*" (Beibl. Bot. Jahrb. 34:3, 1892).

1890: Reiche, in summarizing the family for the Engler and Prantl "Pflanzenfamilien," follows Urban, the only difference being the reduction of the three subgenera of *Sacoglottis* to sections.

1898-1910: Huber describes three new species based on new collections made by either him or Ducke: *Sacoglottis uchi*, *S. duckei*, and *Vantanea cupularis*.

1921: Hallier, in "Beiträge zur Kenntnis der Linaceae," follows Baillon in joining the Humiriaceae with the Linaceae and supports this viewpoint with much data and long considerations. The main difference of Humiriaceae from closely related families, such as Linaceae, is the presence of an intrastaminal free disk, which is usually lacking in Linaceae. But, he says, *Ixonanthes* also contains an intrastaminal disk (according to Pierre in *I. cochinchinensis*).

1922-1938: Ducke, in various papers on Amazon plants, publishes four new species of *Vantanea*, five new species of *Sacoglottis*, several new varieties, and numerous morphologic, ecologic and geographic observations about Humiriaceae. In 1938, he publishes

synopses in key form of the Amazonian *Sacoglottis* and *Vantanea*. Ducke's studies are mainly based on his field experience and large collections, and constitute the largest contribution to our knowledge of the Amazonian flora in this century. Ducke's most outstanding discoveries in *Humiriaceae* are two species—*S. verrucosa* and *S. heterocarpa*—which in the present treatment are credited the rank of new genera.

1922: Berry gives the first description and illustration of a fossil humiriaceous species based on fruit, *Sacoglottis tertiaria*, from the Pliocene horizon in Bolivia.

1924: Berry publishes the first description and illustration of a fossil *Vantanea*, based on well preserved endocarps of the late Eocene or Oligocene of Cipacón, found at 8,185 ft. elevation in Colombia. The endocarps are described as having from five to seven seeds, but what Berry believes to be the seeds ("The stone has imbedded in it from five to seven large seeds") are in fact the valves of the endocarps. This species is named *Saccoglottis cipaconensis*. Other specimens from the Lobitos formation of the Upper Eocene in Peru are attributed to the same species. Another fossil fruit, actually *Sacoglottis*, from the same Cipacón Oligocene formation, is described as *Vantanea colombiana*.

1928: Malme publishes *Sacoglottis mattogrossensis*.

1929: Berry in several papers publishes new data on humiriaceous fossils and describes *Saccoglottis cipaconensis* var. *peruvianus* of the early Tertiary from Belén, Peru, *Vantanea compressiformis* n. sp. from the same locality, and *Vantanea Sheppardi* n. sp. of the Eocene from Ida Seca in Ecuador.

1931: Gleason, in his account of plants of his and other expeditions in Guiana, publishes one species (*H. savannarum*) and one variety (*H. floribunda* var. *spathulata*).

1931: Winkler publishes a new treatment in the second edition of the "Pflanzenfamilien." He follows Baillon and Hallier in considering this group in the Linaceae, but decides to form with it a subfamily, "Unterfamilie Humirioideae." This subfamily is characterized by the intrastaminal disk, the staminal tube, and the thick connective of the anthers. In the treatment he follows Urban's system without making any further contributions to our knowledge.

1933: Reid, in describing *Sacoglottis costata*, a fossil species of the Tertiary in Colombia, emphasizes the structure of *Sacoglottis* fruit and its peculiar dehiscence.

1933: Hill, in an interesting article dedicated to the study of different kinds of germinal dehiscence, gives the first existing information on how the endocarps of *Sacoglottis amazonica* and *S. gabonensis* are dehiscent at germination: "The devices exhibited by the five-ocular

fruits of *Sacoglottis* and *Aubrya* are of similar character, except that in both the valves are of a more spongy nature and ovate in outline, rounded at one end and somewhat pointed at the other, deeply hollowed out on the insides to allow sufficient space for the embryos lying within close to the centre of the fruit" (p. 881).

1934: Macbride describes *Vantanea peruviana* from Peru.

1935: Süssenguth publishes *Humiria cassiquiari* from Venezuela.

1935: The Sixth International Botanical Congress in Amsterdam approves of the inclusion of "*Humiria* St. Hil." (1805), as against "*Houmiri* Aubl.," in the "*Nomina generica conservanda*." The proposal by Lanjouw and Sprague reads: "The correct name for the type genus is *Houmiri* Aubl. (1775). The Latinized form *Humiria* St. Hil. (1805) is so widely employed, however, that it seems desirable to conserve it. Unless this is done, the spelling of the family name will have to be altered."

1938: Weyland publishes a morphologic study of fossil endocarps of *Vantanea* and describes a new species, *Sacoglottis germanica*, which, according to Kirchheimer, is not a Humiriaceae.

1940: Bakhuizen van der Bilt publishes *Sacoglottis kaboeriensis* from Surinam.

1943: Stanley publishes *Vantanea barbourei*, based on an interesting discovery of Barbour that extends the known range of the family northward to Costa Rica.

1945: Ducke describes another Amazonian species, *Sacoglottis ceratocarpa*.

1945: Selling makes the first detailed description of a fossil endocarp of *Humiria* after studying its structure and germinal dehiscence in longitudinal, lingulate valves. He describes the new species *Humiria bahiensis* of the Miocene or Pliocene from the State of Bahia, Brazil, in which specimens show the imprint of two superimposed seeds in a fertile cell. The external picture of the fossil, the cross-section, and the lack of subapical holes are very much suggestive to me of the genus *Vantanea*, but the small size of the endocarp and the two seed impressions incline me to think that Selling is right in considering it a *Humiria*. Selling's work is well illustrated and also gives a picture of *Sacoglottis cipaconensis* Berry and its variety *peruviana* Berry. He discusses this species' generic status and transfers it to *Humiria*, and sees a variety as a species. He believes that the genus is of considerable age and that its distribution in the Tertiary was even wider than at the time of the publication of his paper.

1948: Little publishes *Humiria procera*, based on his collections from the west coast of Ecuador.

1950: Cuatrecasas publishes *Vantanea occidentalis*, *Sacoglottis diguensis* and its variety, *S. melanocarpa*, and *S. ovicarpa*—all of which

are based upon his own collections in the western rainforests of Colombia. These and Little's data extend the known range of the family to the Pacific side of the Andes.

1950: Fróes publishes *Sacoglottis villosa* in Brazil.

1951: Kirchheimer attributes another fossil species to the Humiriaceae, *Sacoglottis kayseri* (Schindehutte) Kirchheimer, which he transferred from *Actinostrobites*. This finding is especially important because the fossil specimens came from Eichelkopf, Homberg Kassel in Germany, this locality signifying a larger area and greater antiquity in the original distribution of the family. He presents morphological descriptions of several known fossils of Humiriaceae and critical and comparative remarks on the three known genera, which he tries to distinguish; but the distinguishing characters used are mainly the existence or absence of resinous cysts, the presence of one or two seeds in each fruit-cell, and the marks or vestiges of vascular bundles. No light is really shed on the actual morphology that distinguishes the endocarps of the three genera. I have serious doubts, because of the illustrations, that the newly transferred *Sacoglottis kayseri* belongs to the Humiriaceae.

1952: Steyermark publishes *Humiria pilosa* from Venezuela.

1956: Cuatrecasas publishes *Vantanea magdalenensis* and a variety of *Sacoglottis* from the Magdalena Valley in central Colombia.

DRIFT FRUIT

Although Aublet's publication in 1775 constitutes the first contribution to the knowledge of humiriaceous plants, unidentified fruit of one species of this family had already been known for about two centuries. These fruit were the woody, ellipsoid endocarps of *Sacoglottis amazonica*, which, filled with empty resinous cavities, had drifted on the ocean currents to the shores of the West Indies and other islands. Found as far away as the Azores and the British Isles, these endocarps had puzzled botanists for almost three centuries. The first written notice of them was published in 1605 by Clusius in his "Exoticorum libri decem" (lib. 2, cap. 4), in which appeared a coarse drawing of the endocarp and a masterpiece of description. Clusius' data were quoted or reproduced by subsequent botanists, such as J. Johnston, J. Bauhin, and H. Sloane. Sloane in 1696 mentioned the abundance of the endocarps found in Jamaica. According to Morris, the specimens collected by Sloane and deposited in the British Museum were recognized by Baker in 1889. In 1884 Morris, at the Palisadoes in Jamaica, collected among other drift fruit those of *Sacoglottis*, which he sent to Kew for determination.

In 1887 Kew received another specimen of the same fruit collected on the shore of Bigborough Bay in southern England. Hillier, assist-

ant at Kew, noticed the great similarity between the drift fruit and specimens of *Sacoglottis gabonensis*, collected by Mann in West Africa; the latter, however, were smaller and more rounded than those of Jamaica and England. Oliver, however, thought that they belonged to *Humiria*, a genus widespread in South America; he wrote: "Until we obtain fruits of *H. balsamifera* we are unable to say whether it is that species or not." In order to attract the attention of people able to help in identifying the Jamaican drift fruit, Morris in 1889 published in "Nature" (pp. 322-323) an article with drawings.

This first article of Morris roused widespread interest and resulted in the discovery of the parental plant of the mysterious fruit. In 1892, Martius identified it as a species of *Sacoglottis*. On several islands and in different countries, people collected and reported the fruit (from Barbados, Dominica, Mustique, St. Vincent, Grenada). The most important fruit was found in Trinidad, where J. H. Hart, Superintendent of the Botanic Gardens, identified Morris' fruit with accurate drawings, by Herman Crueger, a former botanist in Trinidad, of fruit and flowering specimens of a Trinidad tree.

According to Morris (1895, p. 65), Hart wrote in March 1889 as follows: "I am extremely pleased that you called my attention to the Jamaica drift-fruit. I remember the specimens well, and cut several of them in Jamaica at the time we were packing the set you sent to Kew for the Botany of the Challenger Expedition. As soon as I read your article in Nature, I commenced a search among the material in the herbarium here, and found a drawing of *Sacoglottis*, by Crueger, with dissections of the flower and fruit. These made it evident that the plant which produces the unknown fruit is a native of Trinidad. Feeling further interested in the matter, I communicated with Mr. Syl. Devenish, the friend and companion of Crueger on many of his excursions, and I learnt further particulars as follows. When traveling in the forest at Irois, in the southeastern part of the island, they found on the beach specimens of the fruit in question. Following up the stream they came to the tree producing it, from which, I presume, the drawings were taken. In addition, Mr. Devenish gave me a fruit, which I now send, to show there can be no mistake in the matter. This was collected by himself on the spot, so that there can be no doubt of the identity of the species we are both discussing. Mr. Devenish states that the tree is very rare. He saw but two in all his travels through the island. It is known locally as *Cojón de Burro*. It is probable that a greater portion of the drift-fruits found in Jamaica and elsewhere are produced on the mainland of South America, and are brought down by the flood waters of the Orinoco and the Amazon."

Oliver at Kew solved the problem when, receiving Crueger's drawings, he was able to identify them as *Sacoglottis amazonica*. Morris'

second article in *Nature* (1895) is a complete and interesting narration of the earlier and recent history of the Jamaica drift fruit.

In his book "Plants, seeds, and currents," H. B. Guppy (1917) gives an account of his own investigations, conducted independently from those of Morris, on the Jamaica drift fruit. Guppy found endocarps of *Sacoglottis amazonica* on the beaches of Colon, Jamaica, and on Turks Islands, Tobago, and Trinidad. In Trinidad he made the acquaintance of the botanist Hart, who showed him the parental plant species of the then mysterious fruit *S. amazonica* growing in a restricted area of the island. Guppy's book summarizes the history of the drift fruit, and points out that Sloane first recognized this fruit after it had been thrown up on the shores of the northwest islands of Scotland. Guppy emphasized the suitability of *Sacoglottis* endocarps for drifting great distances, and studied possible courses between the Amazon and Orinoco estuaries and the West Indies and Europe via the South Equatorial Current and the Gulf Stream. Stating that *Sacoglottis amazonica* was the only species dispersed by the currents, he pointed out that the currents "would readily transport the fruits in a sound and effective condition from tropical West Africa to Brazil, but not from the tropics of the New World to West Africa."

Ridley in his book "The dispersal of plants" (1930, pp. 203-204) excluded the Humiriaceae from the sea-dispersed plants "as it has failed entirely to cross the sea and establish itself anywhere in Trinidad." But I must say that I cannot agree with Ridley's point of view and still less with that of Guppy. In my opinion, the Humiriaceae are a tropical American indigenous family widespread and rich in forms, whose center of origin was the somewhat elevated lands surrounding the Amazon Basin before the uplifting of the Andes. It is quite clear to me that the single African *Sacoglottis* species, which is very closely related to *S. amazonica*, is an offspring of the Amazon stock; its ancestor at some time in the Tertiary may have found its way along the Brazilian current to establish itself on the West African coast. Furthermore, evidence has established the Amazon and Orinoco origin of the *Sacoglottis* drift endocarps found in the West Indies and British Isles, but no examples of *Sacoglottis gabonensis* have been found on American shores.

The structure of many humiriaceous fruit provides them with empty resinous cysts that make them buoyant, a fact that explains why they drift easily and are often found on the shores of rivers and seas. On the Pacific coast, these fruit were collected and reported by I. M. Johnston at San José Island; they were probably brought there from the western coast of Colombia or from western Costa Rica by the local drifts originated by the Equatorial Counter Current (see

Sacoglottis ovicarpa, p. 168). Very often fruit or endocarps of *Vantanea*, *Sacoglottis*, and *Schistostemon* have been found in drifts and drift deposits of the Amazon and Magdalena Rivers. The abundance of *Vantanea* endocarps in fossil beds proves the drift origin of these deposits and therefore the capacity of currents to transport the *Vantanea* fruits (which lack resinous cavities), especially the mountain rivers with speedy waters.

FOSSILS

About 12 or 13 fossil taxa attributed to the Humiriaceae have been described (see the historical summary above). Except for two described from European specimens, they are from tropical South America—Colombia, Peru, Brazil, and Bolivia—where they were found in Tertiary layers. The most conspicuous species belong to *Vantanea*, others belong to *Sacoglottis*. Much morphologic work on this family has been done by paleontologists and much literature exists, but the genera are not well understood, and many of the published species probably will need transferring. The fossil species published are:

- Vantanea colombiana* Berry from Cipacón, Colombia (Oligocene)
- V. compressiformis* Berry from Belén, Peru (late Eocene)
- V. sheppardii* Berry from Ecuador (Eocene)
- Sacoglottis tertiaria* Berry from Bolivia (Pliocene)
- S. cipaconensis* Berry (*Humiria cipaconensis* (Berry) Selling) from Cipacón, Colombia (Eocene or Oligocene)
- S. cipaconensis peruviana* Berry (*Humiria peruviana* (Berry) Selling) from Belén, Peru (early Tertiary)
- S. costata* Reid from Colombia (Tertiary), probably belonging to *Humiriastrum*
- Humiria bahiensis* Selling from Brazil (Miocene or Pliocene).

Vantanea wilcoxiana Berry, which is based on leaves, has been recently identified by Roland Brown as *Diospyros* sp. According to Kirchheimer, *Sacoglottis germanica* Weyland is identical to *Spondylostrobos smythii* Mueller. On the other hand, I think that *Sacoglottis kayseri* Kirchheimer (*Actinostrobites kayseri* Schindehütte) does not belong to the Humiriaceae. There is no proof at present that the Humiriaceae in Tertiary times spread throughout Europe and Africa; the documentation of living and fossil material supports Berry's belief that the Humiriaceae are an old American stock. This stock evolved and diversified inside the American continent into eight genera and many species widely spread throughout tropical American areas. The only West African species, *Sacoglottis gabonensis*, probably originated from drift fruit brought to Africa from the Amazon regions by ocean currents in earlier Tertiary times.

A revision of the fossil Humiriaceae is necessary. At present Father Gustavo Huertas from Bogotá (Instituto de Ciencias Naturales) is working on this revision.

STRUCTURE OF THE FRUIT

One of the outstanding features of the Humiriaceae is the structure of the fruit. The fruit is drupaceous with a single stone derived from a syncarpous ovary with biovular cells as in *Vantanea* and *Humiria*, or uniovular as in all other genera. The exocarp, which is the whole fleshy layer outside the endocarp, is more or less soft or hard; thick or thin; easily removable at maturity or very adnate to the stone; and hard, granulose, or coriaceous when dry. Usually the surface is smooth but sometimes it is rugate or tuberculate. The endocarp is very hard, woody, with thick walls. Rarely, it has five (also four, six, or seven) seminal cavities, because generally only one or two of the ovary cavities are fertile and developed in the fruit. The cavities are normally monospermous in genera with uniovular ovary cells.

According to my observations on endocarps of different species, in *Vantanea* only one of the two ovules develops into a seed, the fertile cavities being occupied by a single, long, oblong seed. The few notes on *Vantanea* with bispermous loculi that I found in the literature (Selling, 1945, p. 261), are indirect references and not the result of observations. In *Humiria* the endocarp develops a complete cavity for each fertile ovule. When both twin ovules are fertile, we can see two superposed fertile cavities. Often these two cavities are marked outside the endocarp by the curved edges of the valves pinched at the middle. More commonly, only one of the twin ovules and its cavity are developed, the lower one of a carpel alternating with the upper one of the next. The sterile cavities are empty, usually reduced, and sometimes connected with the subapical foramina of the endocarp. Usually not more than four or five ovules are found in a *Humiria* endocarp, more often only two or three, and those of the lower layer. In mature endocarps frequently only fertile cavities are present. The sterile ovary cells become filled with woody wall tissue. Only in *Humiria* are some vacuous sterile loculi often found.

The most interesting peculiarity of humiriaceous fruit is the type of germinal dehiscence of the endocarps. No references to experiments on seed germination in this group exist, but the study of the morphology of the endocarps makes me assume that the single or the few seeds borne germinate without being liberated. The woody endocarp serves as protection to the seed and has a special device to facilitate the liberation of the embryo at germination.

In *Vantanea*, *Duckesia*, and *Humiria* the endocarp shows conspicuous longitudinal lines, or shallow furrows, which mark potential valves stretching from near the apex to above the base. At full maturity, these valves can be removed, like a window shutter or fenestra, from the well-ridged top to the base, continuous with the wall tissue of the endocarp. In *Humiria* it is more difficult to take the valves off artificially. In general sterile valves are more difficult or impossible to remove. At the time of germination, the valves are easily pushed away by the pressure of the developing embryo.

In the above-mentioned genera, the valves have an oblong or tongue shape and have approximately the same width as the alternating costae that separate them. The thick septa of the endocarp form what, for practical purposes, can be called the costae or ribs framing the valves. These costae are more or less at the same level of the valves in the above cited genera. In *Hylocarpa* the costae are very prominent and robust, and separate longitudinal grooves. At the bottom of the grooves the narrower, but also prominent, valves may be seen. In *Endopleura* the prominent and winged ribs comprise five in the lower part; they fork and form 10 woody ribs or wings at the 2 upper thirds. At the bottom of the deep furrows, between the twin costae, lie the narrow, thin, and conspicuous valves. In *Humiristrum* the germinal valves are reduced in size to the upper half of the endocarp.

On the other hand, the endocarps of *Sacoglottis* and *Schistostemon* lack any conspicuous opening device when inspected superficially. The woody septa and walls are usually filled with large globose, resinous cavities, which commonly mark an irregularly bullate surface. On this surface 5 or 10 longitudinal shallow furrows can barely be seen. Only when the endocarps are very much washed and eroded are the 10 thin furrows conspicuous. At late maturity, it is possible, though not always easy, to remove the broad, thick valves on the fertile spots from the rest of the endocarp. These valves are oblong-elliptical, and they cover the space almost from the apex to the bottom. Laterally they are almost adjacent. The intermediate costae are thin, and the septa are almost membranaceous (fig. 1).

The endocarps of *Vantanea*, *Humiria*, *Hylocarpa*, *Endopleura*, and most species of *Humiristrum* are compactly woody, whereas the other genera have many cysts in the woody tissue of the septa, costae, and valves, which in cross section appear to have a spongy appearance. These cavities are secretory sacs, usually empty or with some resinous powder. They provide the fruit with a very buoyant property, for which reason *Sacoglottis* may float and travel for years on rivers and the sea. The larger development of resinous cysts is parallel to the disappearance of fenestra-like valves and the formation of broad, almost

frameless valves. In *Humiriastrum*, most species lack resinous cysts, and only in a few of them are small resinous cavities conspicuous.

Another feature with a possible connection to the embryo liberation is the presence in some genera of small germinal holes at the apex of the endocarp. These holes (foramina) are located on the ribs, near the top. Sometimes they are very deep and may communicate with the seminal cavities. Subapical foramina are especially developed in *Humiria* and *Humiriastrum*. They are also present in *Duckesia* and *Endopleura*.

This type of germinal dehiscence of the endocarps is rare in the plant kingdom. The only similar cases that I have found are those of *Davidia* (Cornaceae) and *Tectonia grandis* (Verbenaceae). The *Davidia* type is the only very close one to *Vantanea*, the former having been well described and illustrated by Hill (1933, p. 884, fig. 12), who

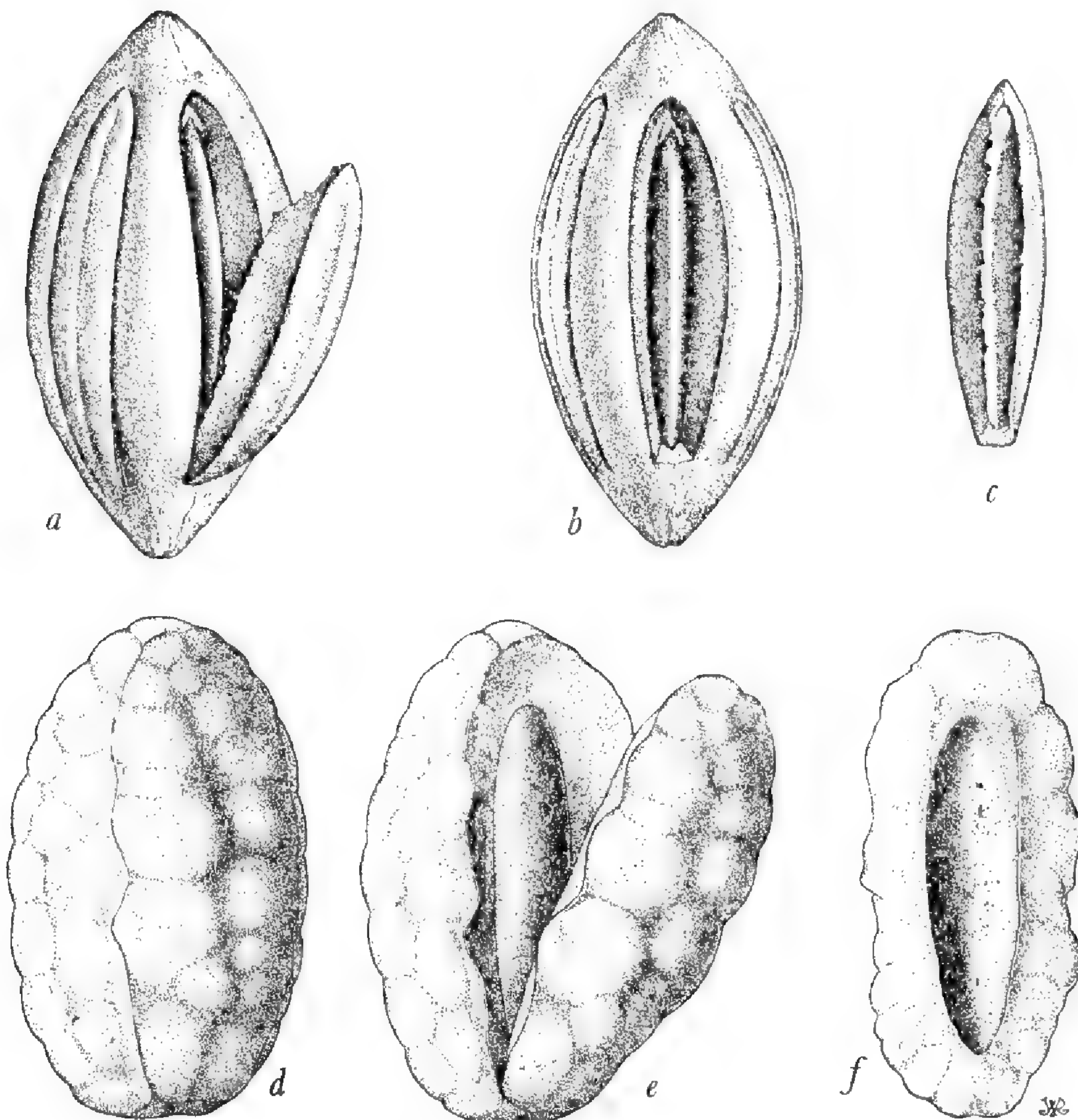


FIGURE 1.—*a-c*, *Vantanea occidentalis*, $\times 1\frac{1}{2}$ (Patiño 12): *a*, endocarp with uplifted valve; *b*, endocarp with valve removed uncovering the seed; *c*, valve from the inside. *d-f*, *Sacoglottis amazonica*, $\times 1$ (Archer 7964): *d*, endocarp, showing the dehiscence line; *e*, endocarp with uplifted valve, uncovering the seed; *f*, valve from the inside.

was the first botanist to describe the dehiscence of *Sacoglottis amazonica* and *S. gabonensis* (p. 881).

RELATIONSHIPS AND EVOLUTION

The basic features of the Humiriaceae as a whole are: Epitropous ovules with micropyle facing upward; free and thick petals; stamens in two or more whorls, united in tube at base; anthers with thick, fleshy, usually elongated connective; intrastaminal free disk surrounding superior ovary; ovary cells 1-2 ovulate; drupaceous fruit with woody, thick endocarp of unique structure with germinal dehiscence and reduction of numbers of seeds to 2 or 1; woody plants with alternate, simple, coriaceous leaves.

These characters place the family in the order *Geraniales*, suborder *Geraniineae* of Engler. Undoubtedly, as first suggested by Planchon, the major affinities of the Humiriaceae are found in the woody members of the Linaceae and the Erythroxylaceae, but not to such an extent as to justify their inclusion in the Linaceae, an inclusion made by Baillon, Hallier, and Winkler. The Humiriaceae form a very natural, homogeneous, and compact group, well-defined and perfectly separable from the Linaceae. The morphology of the fruit, which has shed much light on the definition of the genera in the present work, also shows a basic structure common to the entire family. The endocarps of the Humiriaceae are very different from those of the drupaceous species of the Linaceae. The Linaceae genera closest to the Humiriaceae are *Ixonanthes*, *Ochthocosmus*, and *Ctenolophon* in having a floral disk, but they differ in that the disk is intrastaminal and completely free in Humiriaceae, whereas the stamens are united to the disk (inside or outside) in the three linaceous genera. Furthermore, the flower is perigynous and the fruit a septicidal capsule in *Ixonanthes* and *Ochthocosmus*; the disk is extrastaminal, the ovary bicarpelar, and the style divided in *Ctenolophon*. In all three the anther never has the fleshy, thick connective, typical of the Humiriaceae. In linaceous genera with drupaceous fruit (as in *Hebepetalum* and *Hugonia*), the endocarp is formed by several free pyrena.

The anatomical structure of the Humiriaceae also bespeaks the family rank, as is stated by Heimsch: "Thus, structurally the Humiriaceae are a homogeneous group as evidenced by diffuse porous wood without growth rings; round chiefly solitary vessels with scalariform perforations; heterogenous II A rays; and diffuse parenchyma which generally shows transitions to the abaxial paratracheal type. For this reason the family is described separately rather than as a tribe of the Linaceae as Hallier (33, 34) and Winkler (27) have done. Nevertheless on the basis of the structure of the secondary xylem,

the affinities of the Humiriaceae are more with the Linaceae rather than with any other family" (1942, pp. 96-97, figs. 2-4).

Likewise, Record and Hess write: "In Winkler classification the Humiriaceae are reduced to the status of a subfamily of the Linaceae, but this proposal has little support in the anatomy of the woods" (1943, p. 191). The morphology of the pollen grains differs from that of the general types in the Linaceae. According to Erdtman (1952), the pollen grains in the Humiriaceae are slightly similar to those of certain Celastraceae. The presence of balsamic oils and resins in the bark and fruit of Humiriaceae also distinguishes them from the Linaceae. Hutchinson (1926, p. 196) not only considers the Humiriaceae an independent family, but even places them in the order Malpighiales, in company with Malpighiaceae and Erythroxylaceae; in this placement I concur. In the general treatises, noncritical authors usually follow standard classifications such as Engler's "Pflanzenfamilien." Recent floral works dealing with Humiriaceae treat the group as a family, as do Bakhuizen van den Brink and Pulle in the "Flora of Surinam," and Exell and Mendonça in the "Flora of Angola."

Concerning relationships among the Humiriaceae, one must consider the genus *Vantanea*, with an indefinite number of stamens in several whorls, as the most ancient of the family. Some other older characters are the biovular cells, the bilocular anther thecae, and the narrow, shutterlike valves of the endocarp. The first apparent trend of variation that we can see in the evolution of this family is the reduction of the stamens to a definite number (30, 20, 10). Obviously connected with this reduction is the separation of twin anther sacs in disjunct unilocular thecae and a successive reduction of the four thecae to two. Another evolutionary trend is the reduction of the two ovules in each cell to one. Yet another is the appearance of ribs on the endocarp, a divergence from the almost smooth endocarps of the more primitive forms. Very important evolutionary tendencies are the reduction in length of the germinal opercular valves or, contrarily, the increase in size of the valves, accompanied by substantial decrease of the intermediate costae. In some stages the reduction in size of the valves seems to be compensated by the appearance of apical holes (foramina). The broadening tendency of the valves is parallel to the appearance in the woody tissue of the endocarp of resinous cysts, which are lacking in the primitive forms (*Vantanea*, *Hylocarpa*). The most highly evolved endocarps are more or less bullate and filled with cysts, inconspicuously costate-furrowed, and with broad adjacent germinal valves.

The first lines of variation consisting in the reduction of the number of the stamens with dissociation of the anther twin cells affect all other genera; notwithstanding, the stage with four anther unilocular cells

is kept in only two genera (*Duckesia* and *Endopleura*), all others having the pollen sacs reduced to two. The other basic trend of variation, the reduction of ovules in the ovary cavities from two to one, affects all other genera except *Humiria*. The reduction in length of the endocarp valves is represented by *Humiriastrum* and *Endopleura*; these in turn are provided with subapical foramina. The small genera *Duckesia* and *Hylocarpa*, with lengthwise valvate endocarps, may be considered as more ancient than *Endopleura*. *Hylocarpa* is more evolved than the other two, on the ground of more simplified anthers (with two pollen sacs); *Endopleura* is more advanced on account of the smaller, inconspicuous valves. *Hylocarpa* and *Endopleura* show, in comparison to *Vantanea*, a more advanced form of endocarp in the pronounced furrows and ribs. *Humiriastrum* exhibits an intermediate stage having 20 stamens, short valves limited to the upper half of the endocarp, and subapical foramina. *Schistostemon* and *Sacoglottis* have almost nonfurrowed and nonforaminate, wide-valved endocarps provided with resinous cysts, features typical of the most advanced structure. Furthermore, *Sacoglottis*, having attained the maximum reduction in the androecium (10 stamens), represents the most evolved genus. *Humiria* would remain in an independent line not far from *Vantanea* because of having the primitive number of two ovules and narrow endocarp valves alternating with costae of the same width (see fig. 2).

Most genera of the Humiriaceae are very natural, that is, real. Almost all are extremely homogeneous, the trends of evolution of their species being inconspicuous. However, *Vantanea*, though also natural, has some specific variations that reveal evolutionary tendencies. The oldest type of the genus probably is represented by a species with coriaceous, broad leaves; medium-sized flowers; white, subcoriaceous petals; and smooth or nearly smooth endocarps. This type includes a group (species 1–6) that cover a wide area from Pará to the Pacific coast and to Costa Rica. One trend of evolution diverging from this type could be the reduction in the size and thickness of the leaves, the size of flowers, the number of stamens, and the endocarps, which become smaller and corrugated (species 7 and 8). Another trend is that the flowers become larger and the endocarps corrugated or tuberculate (species 9–13). One of these latter species (*V. guianensis*) exhibits a more advanced degree of evolution through its very large flowers, red petals, and strongly corrugated thick endocarp with a great reduction of the valves, which are inconspicuous from the outside. On the other hand, *V. parviflora* shows another line of evolution, toward a tomentous floral disk and also corrugated endocarp.

I see few connections between ecology and evolutionary variation. The *Vantanea* fruit possibly are eaten by animals and frequently are

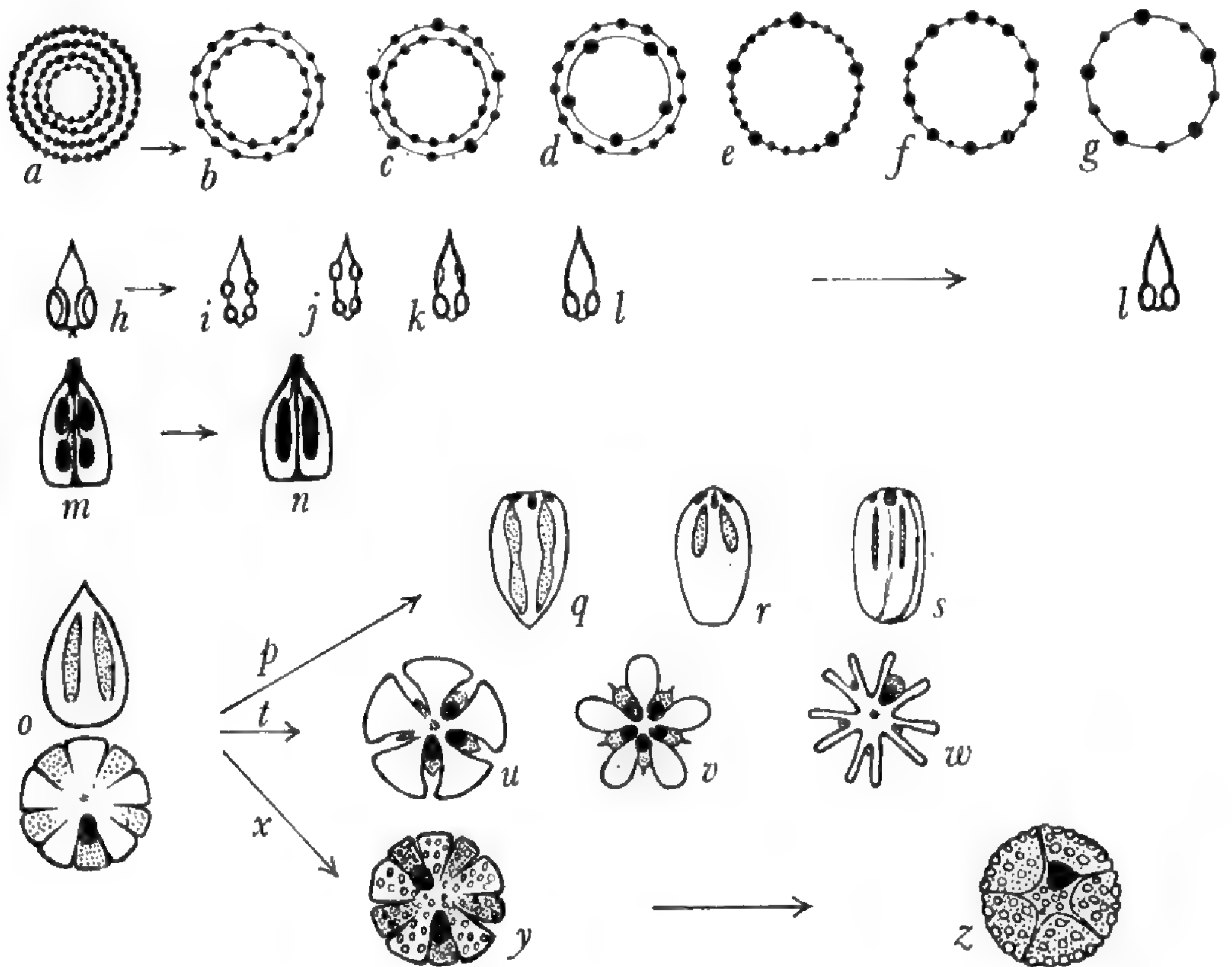


FIGURE 2.—Trends of evolution in Humiriaceae: *a-g*, Androecium, from the multistaminate flower of *Vantanea* to 10-staminate *Sacoglottis*: *a*, *Vantanea*; *b*, *Hylocarpa*; *c*, *Endopleura*; *d*, *Duckesia*, theoretically constructed in two whorls; *e*, *Duckesia* and *Endopleura* in one whorl as it appears; *f*, *Humiria*, *Humiristrum*, *Schistostemon*; *g*, *Sacoglottis*. *h-l*, Anthers: *h*, *Vantanea*, 2 bilocular anthers; *i-j*, *Duckesia*, *Endopleura*, 4 unilocular disjuncted anthers; *k*, 4 unilocular anthers with sterile upper sacs, transition to *l*, as in all other genera. *m-n*, Ovary: *m*, loculi biovular, *Vantanea*, *Humiria*; *n*, loculi uniovular, the other genera. *o-z*, Endocarp: *o*, shape and section of typical *Vantanea*, from which derive three tendencies: 1, *p*, Appearance of apical foramina and reduction in length of valves as in: *q*, *Humiria*; *r*, *Humiristrum*; *s*, *Endopleura*. 2, *t*, Reduction of valves in width and enlargement of costae as in: *u*, *Vantanea guianensis*; *v*, *Hylocarpa*; *w*, *Endopleura*. 3, *x*, Appearance of resinous cysts, enlargement of valves with reduction of costae as in: *y*, *Duckesia*; *z*, *Sacoglottis*, *Schistostemon*.

transported by rivers. The development of more buoyant endocarps (in *Duckesia*, *Sacoglottis*, and *Schistostemon*) could be favored in species more likely to live in low regions and flooded lands. On the other hand, species of *Humiria*, which are more widely spread throughout the mountains, have small, juicy, fleshy fruit more suited to being spread by birds; the endocarps lack resinous cavities.

Family Humiriaceae

Humiriaceae Jussieu in St. Hil. Fl. Bras. Merid. 2:87. 1829.

Ordo XXXV Humiriaceae, Benth. & Hook. Gen. Pl. 1:246-247. 1862.

Linacearum Series Houmirieae, Baill. Adansonia 10:368, 371. 1873.—Hist. Pl. 5:51, 56. 1874.

Humiriaceae (Familia), Urban *in* Mart. Fl. Bras. 12(2):425–454, pls. 92–96. 1877.

Humiriaceae (Familie), Reiche *in* Engl. & Prantl, Pflanzenfam. 3(4):35–37, fig. 32. 1890.

Humirioideae (Unterfamilie), Winkler *in* Engl. & Harms, Pflanzenfam. 19a:126–130, figs. 58, 59. 1931.

DESCRIPTION: Flowers hermaphroditic, complete, actinomorphic. Sepals 5, persistent, thick and carnose at base, thinner toward margin, suborbicular or triangular, more or less connate in tube or cupule, glabrous, pubescent or tomentous outside, sometimes with marginal or dorsal glands; estivation quincuncial or imbricated; all same size or 2 outer ones smaller. Petals 5, deciduous or sometimes persistent, free, thick or membranaceous, usually 3–5-nervate, oblong, linear or oblong-lanceolate, acute to obtuse, rarely with gland at top, margin smooth, sometimes with tooth at 1 side near apex, above glabrous, below glabrous or pilose, white, greenish white, or yellowish white, rarely red; estivation contorted, cochlear or quincuncial, indistinctly dextrorse or sinistrorse. Stamens monadelphous, numerous (indefinite) and pluriseriate or in definite number, 30–10 and 1–2 seriate. Filaments filiform (when numerous), slender and flexuose, or thick, complanate, linear, acute at apex, straight and glabrous or papillose; at base connate in more or less long tube, alternating in different lengths, sometimes the 5 alternating with the petals are trifurcate at apex and triantheriferous. Anthers dorsifixed or subbasifixed; thecae 2, bilocular, laterally attached, ellipsoid-oblong and each cell dehiscing by longitudinal slit, or 4, unilocular, rounded or ellipsoid disjunct thecae (2 lateral and 2 basal), dehiscing by detachment, or 2 unilocular, disjunct, basal, dehiscing by detachment; connective thick, fleshy, ovoid or lanceolate, obtuse at apex or most commonly produced in apiculum or linguiform appendix. Sometimes some filaments lack anther; occasionally smaller, sterile filaments (staminodia) present. Pollen grains usually 3-colporate, also 4-colporate, suboblate, oblate-spheroidal, prolate-spheroidal (27×32 , 31×35 , $33 \times 3\mu$), exine not verrucose, tenuisexinous (Erdtman). Intrastaminal free disk girding ovary, membranaceous or subcoriaceous, tubular or cupular, dentate, lobate, laciniate or composed of 10–20 free scales. Gynoecium syncarpous, carpels 5 (rarely 4, 6, or 7), opposite sepals or alternate. Ovary ovoid or ellipsoid, sessile, 5 (4, 6, 8) septate with axile placentation, cells uniovulate or biovulate. Style single, entire, columnar, erect, as long as stamens or shorter, rarely longer. Stigma narrowly or broadly capitate, 5-lobate or 5-radiate. Ovules anatropous, epitropous with 2 integuments, pending at inner angle of ovary cells, micropyle pointing upward, raphe ventral; when 2 ovules present in each cell, superposite and lower one hanging from longer funiculus. Fruit drupaceous from size of pea to that of mango;

exocarp hard-fleshy varying from pulpy to fibrous, subcoriaceous texture. Endocarp (putamen) woody, usually very hard, compact or with many resin-filled, round cavities, rarely spongy-woody, 5 (4, 6, 7) septate, commonly with only 1–2, rarely 3, 4, or 5 seeds developed; surface smooth, bullate, rugose, or tuberculate, slightly striate or strongly costate; with germinal dehiscence, provided with as many longitudinal opercula or valves as carpels, which may open or be pushed away by emerging embryo at germination of seed inside fruit. Often subapical foramina are present. Seeds oblong with double testa, exterior often adherent to putamen, inner membranaceous, thin; embryo straight or slightly curved, cotyledons oblong or ovate, often subcordate at base, radicle half as long, endosperm fleshy and oily.

Woody, evergreen plants from small shrubs to large trees; wood reddish, hard, often with balsamic juice. Leaves alternate, simple, often distichous, coriaceous or subcoriaceous, penninerved, entire, crenulate or slightly serrate, petiolate or rarely sessile, sometimes decurrent along branches, often punctate-glandulose near margin on underside, marginal teeth when young often aculeate, later callous-tipped. Stipules very small, geminate, deciduous or lacking. Inflorescences axillary, pseudoterminal or rarely terminal, paniculate, often corymbiform, of dichasial type and trichotomous, but through reduction often with dichotomous or alternate (cincinnate) branching; branchlets often with incrassate ends, articulate. Pedicels short, articulate. Bracts and bracteoles persistent or deciduous, small, amplexant. Wood, according to Record and Hess: "Heartwood grayish brown to reddish or purplish brown; distinct but not sharply demarcated, from the sapwood. Luster usually low. Odorless and tasteless when dry. Hard and heavy to decidedly so; sp. gr. (air-dry) 0.80 to 1.10; weight 50 to 69 lbs. per cu. ft.; texture medium to coarse; grain mostly irregular; not easy to work; is tough and strong; finishes smoothly; durability doubtful." For further technical characteristics, see Record and Hess, p. 191–192, 1943; see also figure 3.

DISTRIBUTION: A typical tropical family with 8 genera, 49 species, and many subspecies, varieties, and forms. They are important constituents of the Tropical American rain forests as well as of the subhygrophytic formations of the savannas, campos, restingas, and caatingas extending from Costa Rica to southern Brazil. Only one species is found outside America, on the West African coast. This distribution is shown in figure 4.

The fossil remains of *Vantanea* found at the west coast of Peru (Belén, Piura) indicate not only that a wider distribution of the

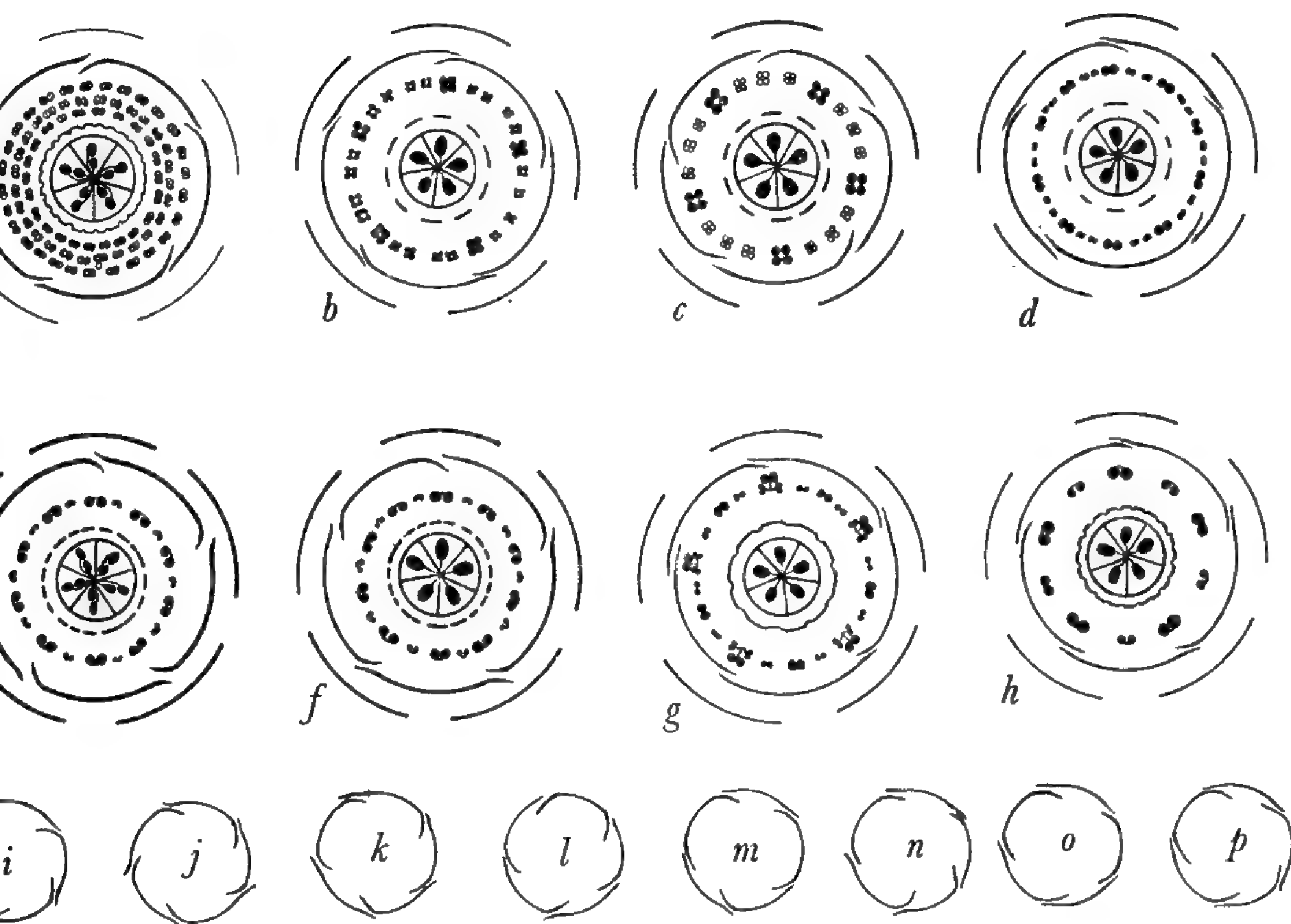


FIGURE 3.—Floral diagrams of Humiriaceae: *a*, *Vantanea*; *b*, *Endopleura*; *c*, *Duckesia*; *d*, *Hylocarpa*; *e*, *Humiria*; *f*, *Humiristrum*; *g*, *Schistostemon*; *h*, *Sacoglottis*; *i*–*p*, different kinds of aestivation of the corolla found in Humiriaceae. In *c* and *d* the white circles represent sterile stamens; in other diagrams some of the smaller stamens are often also sterile.

family existed in the Eocene, but also that the mentioned arid region was rainy and covered with rain forest during Tertiary times.

According to Croizat (1952, p. 388), the Humiriaceae belong to a Genorheithrum of Gondwanic origin and reached the Americas from the east. Andean fossils prove that abundant earlier populations in that region were deeply disturbed by the uplifting of the Andes, and that the Humiriaceae existed in the New World long before the Tertiary.

ECONOMIC USES: The bark and wood of some species and varieties of *Humiria* produce the “umiri” or “umiry-balsam,” with properties similar to those attributed to the Copaiva and Peruvian balsam. Little is known about its preparation, trade, and chemical composition (Wiesner, 1927, p. 1040; Wehmer, 1929, p. 597; Urban, 1887, p. 453). The exocarp of the fruits of Humiriaceae is more or less fleshy and in some species edible, as in many *Humiria* varieties and in some of *Sacoglottis* and *Vantanea*. The exocarp and seeds contain a fatty oil that in some places of the Amazon is used in the domestic economy. The oil of “uchi” has organoleptic properties similar to those of

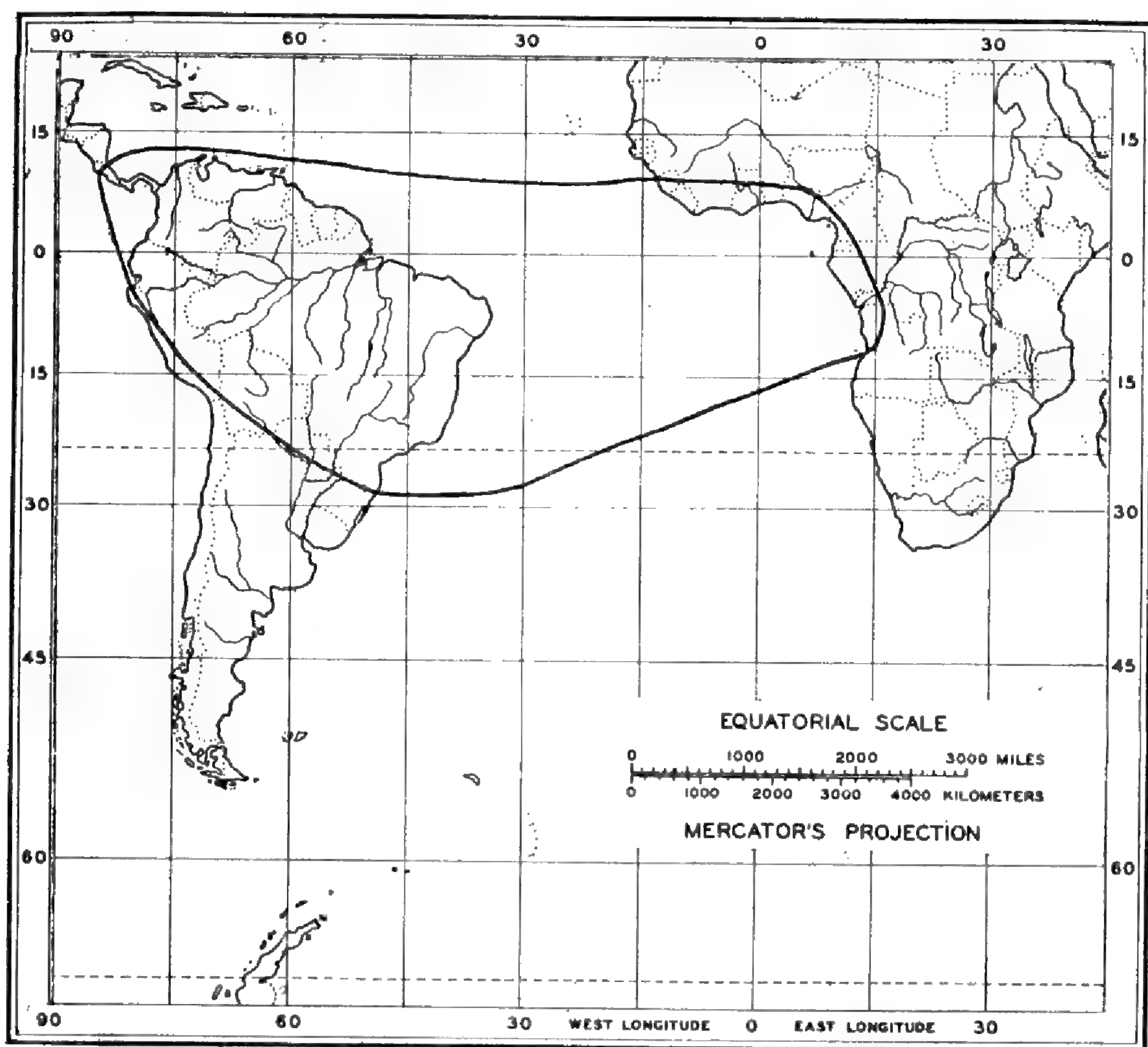


FIGURE 4.—Worldwide distribution of the family Humiriaceae.

olive oil (Pereira Pinto, 1956). The seeds of *Sacoglottis gabonensis* contain 54 percent fatty oil (Wehmer, 1929, p. 597; Wiesner, 1927, p. 743).

The wood of the Humiriaceae is hard and used locally in construction work. Metcalf and Chalk (1950, pp. 277–279) wrote about its economic uses thus: “The timbers of this family are dense; they are of little importance though some species of *Humiria* are used in tropical America for heavy construction, wheels, etc.”

Key to the Tribes and Genera of Humiriaceae

1. Stamens 50–180; anthers with 2 bilocular thecae: Tribe VANTANEOIDEAE.
Connective of anthers acute. Carpels opposite sepals, 2-ovulate. Endocarp with lingulate valves **1. Vantanea**
1. Stamens 10–30; anthers with unilocular, free thecae: Tribe HUMIRIOIDEAE.
 2. Anthers with 4 unilocular thecae; connective acute. Carpels opposite sepals, 1-ovulate.
 3. Endocarp spongy-lignose, evenly costate with long, lingulate valves, resinous-lacunose. Stamens 20–25 **2. Duckesia**

3. Endocarp prominently, sharply costate and furrowed with shorter, inconspicuous valves at bottom of furrows; compact-woody, not resinous-lacunose. Stamens 20–30. **3. Endopleura**
2. Anthers with 2 unilocular thecae.
 4. Stamens 30, anthers with thick, very obtuse connective; thecae basal, glabrous. Endocarp strongly costate. valvate at furrows, compact-woody, not resinous-lacunose **4. Hylocarpa**
 4. Stamens 10–20, anthers with attenuate, acute connective (very rarely obtuse).
 5. Thecae of anthers basal, pilose. Carpels opposite petals, 2-ovulate. Endocarp woody, striate, evenly costate-valvate, 5-foraminate at apex, not resinous-lacunose, valves linear, oblong or lingulate.
 5. **Humiria**
 5. Thecae of anthers glabrous. Carpels opposite sepals, 1-ovulate.
 6. Stamens 10. Thecae of anthers inferolateral. Endocarp shallowly or inconspicuously furrowed, not foraminate at apex, resinous-lacunose, valves broad, adjacent, alternating ribs thin, inconspicuous **8. Sacoglottis**
 6. Stamens 20.
 7. Episepalous stamens 5, longer, trifurcate at apex, triantheriferous. Epipetalous stamens 5, medium-sized, entire, monantheriferous. Ten shorter alternate stamens monantheriferous. Thecae of anthers inferolateral. Endocarp shallowly or inconspicuously furrowed, not foraminate at apex, resinous-lacunose, valves broad, adjacent, alternating ribs inconspicuous.
 7. **Schistostemon**
 7. All 20 stamens monantheriferous, 10 episepalous and epipetalous longer than alternating ones. Thecae of anthers basal. Endocarp 5-foraminate at apex, with 5 alternating descending, oblong and short opercular valves. **6. Humiriastrum**

Tribe Vantaneoideae

Vantaneoideae Cuatr., tribus nova Humiriacearum.

Stamina numerosa antheris thecis duobus bilocularibus loculis rimoso-dehiscentibus. Genus typicum *Vantanea* Aublet.

1. *Vantanea*

Vantanea Aubl. Pl. Guian. 1:572, pl. 229. 1775.—Lam. Encycl. 8:334, pl. 471. 1808.—Benth. in Hook. Journ. Bot. Kew Misc. 5:98. 1853.—Benth. & Hook. Gen. Pl. 1:246. 1862.—Urb. in Mart. Fl. Bras. 12(2):450. 1877.—Reiche in Engl. & Prantl, Pflanzenfam. 3(4):37, fig. 32. 1890.—Winkl. in Engl. & Harms, Pflanzenfam. 19a:106, 128, fig. 59. 1931.—Lemée, Dict. Descr. Synon. Gen. Phan. 6:832. 1935.

Lemniscia Schreb. Gen. Pl. (8 ed.) 1:358. 1789.

Lemniscia Willd., Sp. Pl. 2:1172. 1800.—Pers. Syn. Pl. 2:70. 1807.

Helleria Nees & Mart. Nov. Act. Acad. Nat. Cur. 12:38, pl. 7. 1824.—Mart.

Nov. Gen. et Sp. 2:147. 1827.—Juss. in St. Hil. Fl. Bras. Merid. 2:91.

1829.—Endl. Gen. Pl., 1040. 1840.—Baill. Adansonia 1:209. 1860.

Houmiri Sect. *Vantanea* Baill. Adansonia 10:370. 1870.—Hist. Pl. 5:48, figs. 96, 97. 1874.

Houmiri Sect. *Vantaneoides* Baill. Adansonia 10:370. 1870.—Hist. Pl. 5:48. 1874.

Type species: *Vantanea guianensis* Aublet.

Calyx cupular with 5 sepals more or less united up to a subentire margin. Petals 5, free, thick, oblong or linear, the estivation contorted. Stamens 50–120, sometimes more (up to 180), in 3 or 4 rows, the filaments thin, glabrous, flexuose, inferiorly connate in a tube surrounding the ovary. Anthers ovate-lanceolate, affixed near the base; thecae 2, bilocular, ellipsoid, attached at the lower side, each cell dehiscent by a longitudinal cleft; the connective thick, ovate-oblong, acuminate, acute, or subobtuse. Disk cupular dentate or fimbriate, girdling the ovary. Carpels opposite the sepals, biovulate. Ovary 5-locular, the two ovules in each cell anatropous, with

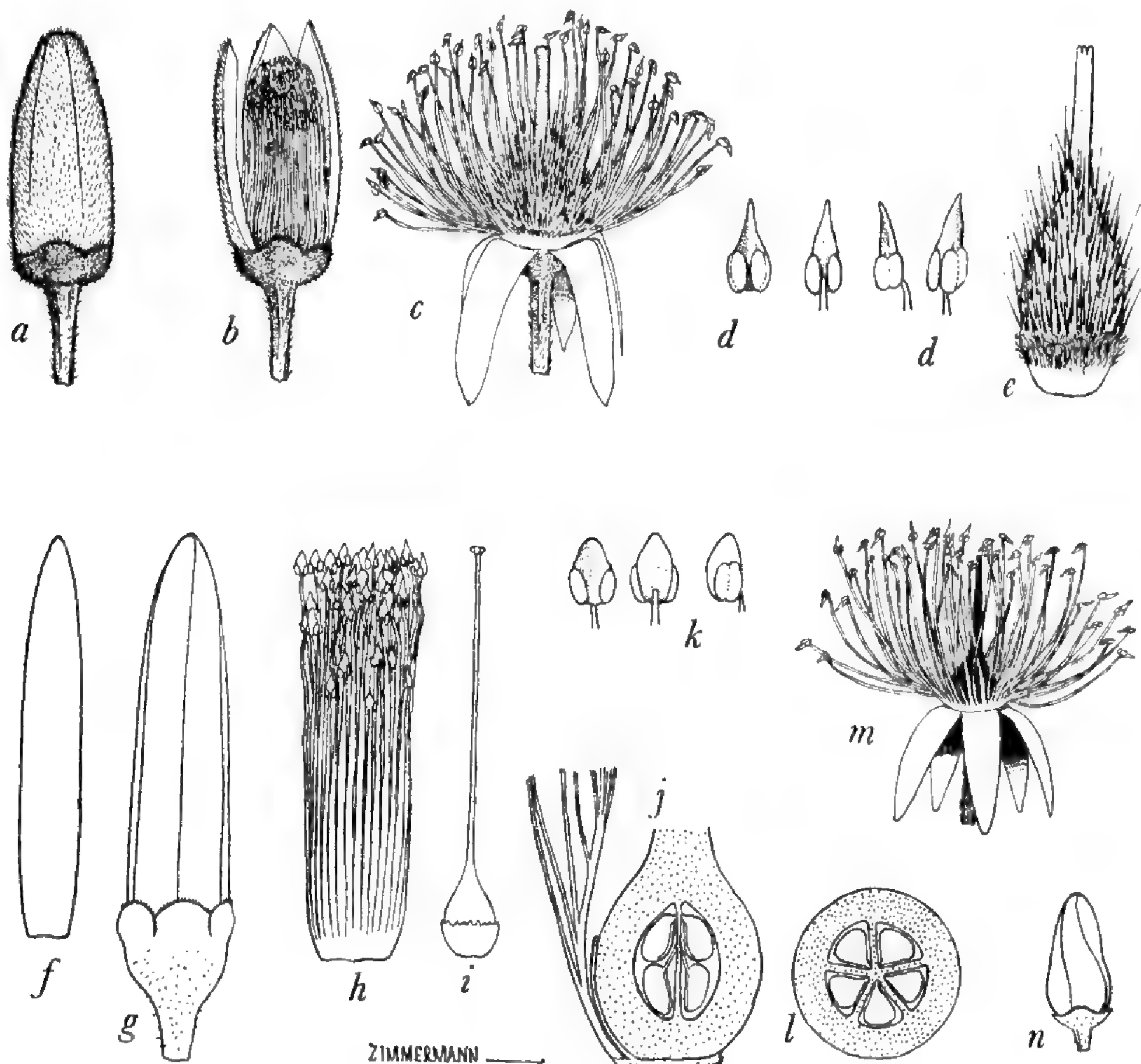


FIGURE 5.—a-e, *Vantanea parviflora*: a, bud, $\times 2\frac{1}{2}$; b, open bud showing the androecium; c, open flower, $\times 2\frac{1}{2}$ (Ducke 23425); d, anthers, $\times 10$; e, gynoecium surrounded by the disk, $\times 10$ (Schultes & Lopez 9267). f-l, *Vantanea minor* (Tamayo 3123): f, petal, $\times 2\frac{1}{2}$; g, bud, $\times 2\frac{1}{2}$; h, androecium, $\times 2\frac{1}{2}$; i, gynoecium surrounded by the disk, $\times 2\frac{1}{2}$; j, longitudinal section showing the staminal tube, disk, and ovary, $\times 7\frac{1}{2}$; k, anthers, $\times 10$, inner, outer, and lateral view; l, transection of the ovary, $\times 7\frac{1}{2}$. m-n, *Vantanea micrantha* (Ducke 751): m, open flower, $\times 2\frac{1}{2}$; n, bud, $\times 2\frac{1}{2}$.

ventral raphe, hanging superposed from the inner angle, the lower one with long funiculus. Style erect, attaining or exceeding the stamens. Stigma more or less thickened, 5-lobate. Drupe medium-sized or large, smooth, ovoid or ellipsoid, the exocarp carnose, subcoriaceous when dry, thick or thin. Endocarp woody without resiniferous cavities, dehiscent at germination of the seeds by longitudinal,

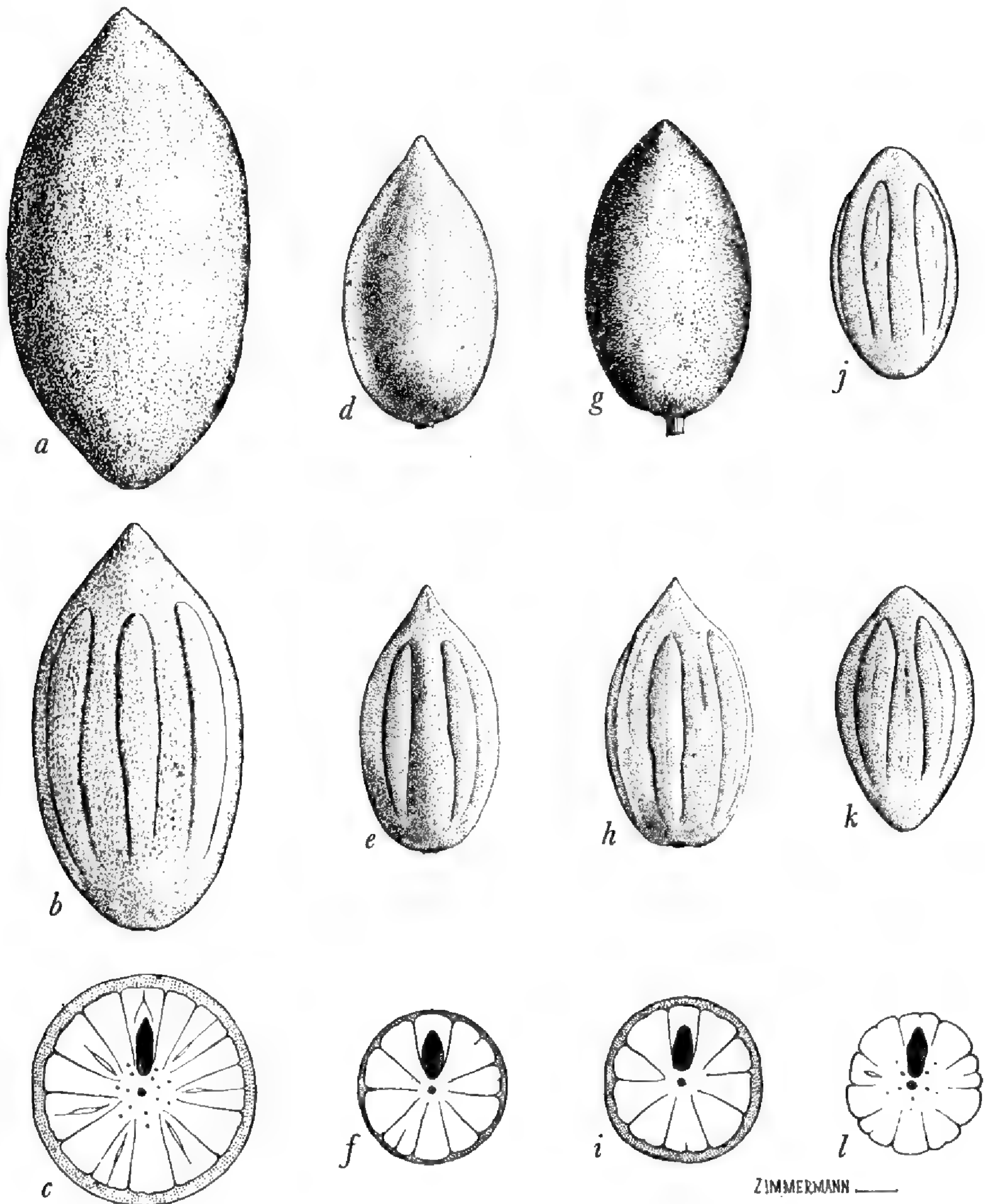


FIGURE 6.—*Vantanea*, fruit, $\times 1$: a-c, *Vantanea paraensis* (Ducke 23430): a, fruit; b, endocarp; c, transection. d-f, *Vantanea celativenia* (Krukoff 7182): d, fruit; e, endocarp; f, transection. g-i, *Vantanea magdalenensis* (Lamb 133): g, fruit; h, endocarp; i, transection. j, *Vantanea barbourii* (Barbour 1018), endocarp. k-l, *Vantanea occidentalis* (Patiño 12): k, endocarp; l, transection.

linear or oblong valves or opercula, which are pushed away by the emerging radicle of the embryo. Usually only 1 seed develops in each cell and only 1 (rarely 2 or 3) can be counted in each fruit. Evergreen trees with coriaceous or subcoriaceous, simple, alternate, petiolate, or sessile leaves. Inflorescences axillary and terminal, paniculate, usually dichotomous, also with alternate branching. Bracts deciduous. (See also figs. 1, 3, and 5-7.)

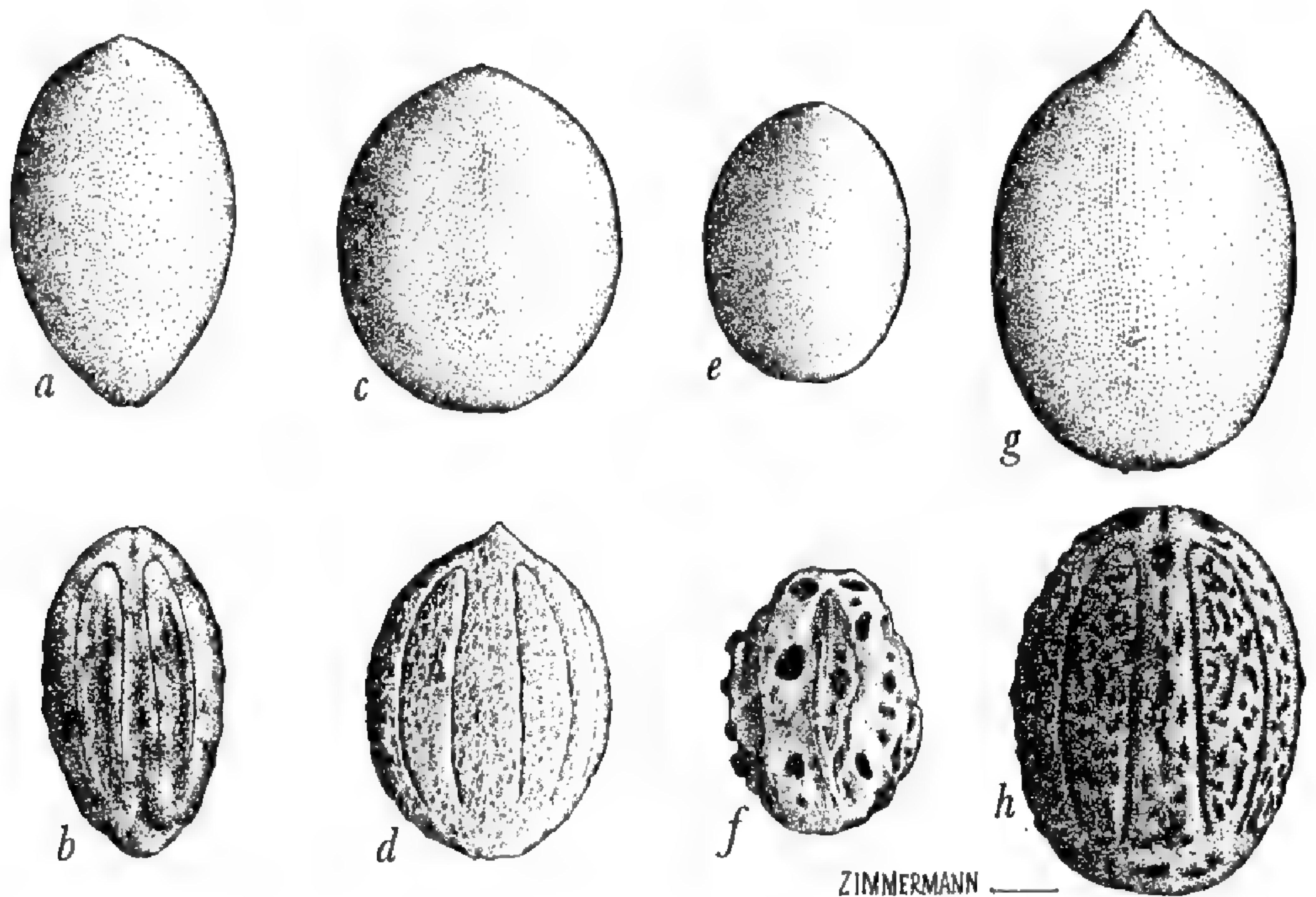


FIGURE 7.—*Vantanea*, fruit, $\times 1$: *a-b*, *Vantanea compacta* (Ducke 1513): *a*, fruit; *b*, endocarp. *c-d*, *Vantanea parviflora*: *c*, fruit (Ducke 23425); *d*, endocarp (Ducke 23426). *e-f*, *Vantanea micrantha* (Ducke 30135): *e*, fruit; *f*, endocarp. *g-h*, *Vantanea minor* (Bernardi 2613): *g*, fruit; *h*, endocarp.

Vantanea comprises 14 species spread throughout the tropical rain forests, from the Brazilian State of Santa Catarina (its southern limit) to Costa Rica in Central America. Most of the species are endemic to limited regions. They grow at low altitudes, though not in flooded areas, and can be found on mountains up to 800 m. elevation in the Guianas. Except for *V. guianensis*, which exhibits large, red, or red-purple petals, the flowers are white or whitish.

The name “*Vantanea*” is derived from the Caribbean name “*iovantan*,” which is given in French Guiana to *Vantanea guianensis*.

Key to the Species of *Vantanea*

1. Fruit with smooth pericarp.
 2. Disk tomentose. Ovary hispid-villose. Drupe ellipsoid, $2.5-2.8 \times 2.2-2.5$ cm. Endocarp very rugose, $2.1-2.5 \times 1.8-2$ cm. Petals white.
 14. *V. parviflora*

2. Disk glabrous.

3. Ovary more or less tomentose or hirsute. Petals white above.

4. Leaf blades small, $3.5-7(-9) \times 1.3-2.5(-4)$ cm. oblanceolate or lanceolate-elliptic, rarely oblong-elliptic. Endocarp rugulose.

10. *V. compacta*

5. Drupe obovate-ellipsoid, oblong, rounded at apex, narrowed at base, $2.4-2.8 \times 1.5-1.8$ cm. Endocarp oblong-ellipsoid, about 2.5×1.4 cm 10a. *V. compacta* subsp. *compacta*

5. Drupe globose-ovoid, subrounded or obtuse at apex, rounded at base, $1.6-1.8 \times 1.4-1.6$ cm. Endocarp subglobose-ovoid about 1.7×1.4 cm 10b. *V. compacta* subsp. *microcarpa*

4. Leaf blades larger, $4-19 \times 2.5-10$ cm., ovate or obovate, also elliptic. Endocarp smooth or nearly so (unknown in *V. obovata*).

6. Petals pubescent or tomentose outside.

7. Petiole 2-4 mm. long. Ovary oblong, glabrous on lower third, villose above. Disk membranaceous, tubular 1-3 mm. high. Leaf blades obovate, large ($10-19 \times 6.5-10$ cm.). Petals $5.5-6 \times 2.5$ mm. Endocarp oblong-ovoid, rounded at base, acute at apex 1. *V. magdalenensis*

7. Petiole 6-12 mm. long. Ovary ovoid, long-tomentose-hirsute. Disk rather thick, cupular, less than 1 mm. high. Leaf blades elliptic or obovate, small ($4-12 \times 2.4-8$ cm.).

8. Petals 10-13 mm. long. Branchlets of inflorescence densely tomentose-hirtous. Stamens more than 100, 6-9 mm. long.

2. *V. obovata*

8. Petals about 7 mm. long. Branchlets of inflorescence short-tomentulose-hirtellous. Stamens 50-60, 5-7 mm. long. Endocarp oblong-ellipsoid, obtuse at both ends, 2.7×1.6 cm.

3. *V. barbourii*

6. Petals glabrous.

9. Petioles 1-5 mm. long. Ovary densely long-hirsute-lanate. Petals about 9 mm. long. Drupe ovoid-ellipsoid, 3.5×1.8 cm. long. Endocarp ellipsoid-attenuate at both ends, $3-3.3 \times 1.5-1.7$ cm 4. *V. occidentalis*

9. Petioles 10-20 mm. long.

10. Drupe oblong-ellipsoid, $5-5.3 \times 2.8-3$ cm. Endocarp ellipsoid-oblong, obtuse at both ends, 4.6×2.5 cm. with 7 valves. Exocarp 2 mm. thick. Ovary short-velvety-tomentose. Petals 6-8 mm. long 5. *V. paraensis*

10. Drupe ovoid-ellipsoid, $3 \times 1.6-1.7$ cm. rounded at base, acute at apex. Endocarp ovoid-ellipsoid, rounded at base, acute or apiculate at apex, $2.8-3 \times 1.6$ cm. with 5 valves. Exocarp 0.5 mm. thick. Flowers unknown . 6. *V. celativenia*

3. Ovary glabrous. Petals glabrous.

11. Inflorescence glabrous. Flowers 25-40 mm. long. Petals red, 25-35 mm. long. Stamens 26-35 mm. long, tube 5-8 mm. high. Anther cells oblong, 0.8 mm. long, the connective with short, acute tip. Calyx 4 mm. high, lobes glandular outside. Petioles 6-12 mm. Pedicels 2-5 mm. 13. *V. guianensis*

11. Inflorescence more or less densely tomentulose-hirtellous. Flowers smaller, petals white or whitish, less than 15 mm. long.

12. Flowers small, petals 4-5 mm. long. Calyx 0.6-0.7 mm. high, papillose outside, margin ciliate. Leaf blades thin, flexible,

- lanceolate or lanceolate-elliptic, 5–12×2–5 cm. Petioles 3–8 mm. long. Disk 1–2 mm. high more or less laciniate. Drupe medium-sized 20–25×14–22 mm. Endocarp strongly corrugate-sulcate, 20×16 mm. 7. **V. micrantha**
12. Flowers larger, the petals 10–14 mm. Leaf blades rigid, coriaceous.
13. Blades large (10–20×5–10 cm.). Petioles 6–12 mm. Calyx pubescent-hirtellous. Disk 1.8 mm. high, laciniate. Anther-connective elongate, subacute. Drupe large, ellipsoid (5–10×3.5–4.5 cm.). Endocarp anfractuose-rugose.
11. **V. macrocarpa**
13. Blades smaller (3–8×1.2–4.5 cm.), rigid. Petiole 1–4 mm. Calyx glabrous. Disk short (1 mm. high), denticulate.
14. Petals 12–14 mm. long. Stamens 9–12 mm. long, tube 3–4 mm. high. Anther-connectives short, thick, obtuse. Drupe smooth 3.5–5×2.2–3 cm. Endocarp densely anfractuose-rugose, 3–4×2–3 cm. Petiole 1–2 mm. long 8. **V. minor**
14. Petals about 11 mm. long. Stamens 7–10 mm. long, tube 1–1.5 mm. high. Anther-connective elongate, subobtuse. Drupe unknown. Petioles 3–4 mm. long . . . 9. **V. peruviana**
1. Fruit with strongly tuberculate, warty pericarp, 6–8 cm. long 4–6 cm. broad. Exocarp 8–10 mm. thick. Endocarp anfractuose-rugose, cavernous.
12. **V. tuberculata**

1. **Vantanea magdalenensis** Cuatr., Brittonia 8:195. 1956.

FIGURE 8, a–c

Type: *Lamb* 133, Colombia, Magdalena valley.

Large tree; terminal branchlets subterete, greenish, lenticellate, glabrous. Leaves rather thick coriaceous, glabrous. Petioles thick, 2–4 mm. long. Blades entire, obovate, oblong-obovate or obovate-elliptic, more or less narrowed, obtusely cuneate or subrounded at base, rounded or very obtuse at apex, 11–19 cm. long, 6.5–10 cm. broad; brownish above when dry, the midrib conspicuous, secondary nerves filiform, minor veins obsolete; pale brown beneath and with very prominent midrib, 8–10 prominent secondary nerves on both sides, subspreading, near margin arched, ascending, anastomosed, and slender, minor nerves prominulous and loosely reticulate.

Inflorescences at end of branchlets, paniculate, shorter than upper leaves; branches and branchlets dichotomously articulate, hirtellous-tomentose. Bracts deciduous. Pedicels thick, tomentose, about 1 mm. long. Calyx when open 3 mm. diameter, lobes rounded, 1 mm. long, pubescent outside. Petals obovate-linear, rather thick, 5.5–6 mm. long, 2.5 mm. broad, tomentose outside. Stamens many, about triseriate, unequal, filaments glabrous, united in a ring 1–2 mm. high. Anthers minutely ovate-rhomboid, 4-lobed, the connective thick, attenuate toward the apex. Disk tubular, membranous, eroded at margin, 1–3 mm. high. Ovary oblong, 3 mm. high, the lower third glabrous, pubescent above. Styles filiform, glabrous, 2 mm. long. Drupe subovate-elliptic, rounded at base, slightly narrowed at apex,



FIGURE 8.—*a*, *Vantanea magdalenensis*, $\times \frac{1}{3}$ (Lamb 133); *b*, *Vantanea magdalenensis*, bud, $\times 1\frac{2}{3}$; *c*, *Vantanea magdalenensis*, petal, $\times 1\frac{2}{3}$; *d*, *Vantanea obovata* (Glaziou 18963); *e*, *Vantanea obovata*, bud, $\times 1\frac{2}{3}$.

about 3.2 cm. long, 2 cm. thick. Exocarp gray when dry, 1 mm. thick, minutely velutinous-tomentose. Endocarp woody, about 2.8×1.8 cm., broadly rounded at base, acute at apex, surface slightly rugulose, practically smooth, with 5 marked ribs and 5 oblong, 2.5-cm.-long, 5-mm.-wide valves.

V. magdalenensis is the only species of the genus found in the interior valleys of Colombia. It is a large tree of the upland rain forests. Its distribution is limited to the Magdalena Valley.

COLOMBIA: SANTANDER: Valle del Magdalena, Cimitarra, km. 3 de la carretera del Ermitaño, 24-VII-1954, "macabalo," Lamb 133 (US, holotype; COL, isotype).

2. *Vantanea obovata* (Nees & Mart.) Benth. in Hook. Journ. Bot. Kew Misc. 5:99. 1853.—Urb. in Mart. Fl. Bras. 12(2):451. 1877. FIGURE 8, *d-e*
Helleria obovata Nees & Mart. in Mart. Nov. Act. Acad. Nat. Cur. 12:40, pl. 7. 1824.—A. Juss. in St. Hil. Fl. Bras. merid. 2:91, pl. 504. 1829.
Helleria ovalifolia A. Juss. in St. Hil., *ibid.*: 91. 1829.
Vantanea ovalifolia Benth. in Hook. Journ. Bot. Kew Misc. 5:99. 1853.

Types: *Martius*, Brazil, Minas Geraes, Tejuco. *St. Hilaire*, Bomfin, Brazil, Minas Geraes, Minas Novas (type of *Helleria ovalifolia* Juss.).

Tree with subterete, granulate-lenticellate, glabrous or scarcely puberulous, terminal branchlets. Leaves rigid, coriaceous, glabrous. Petioles 6–12 mm. long, subterete more or less sulcate above. Leaf blades entire, obovate or obovate-elliptic, obtusely or acutely cuneate at base, rounded or very obtuse and often retuse at apex, 4–10 cm. long, 2.5–6 cm. wide; above lustrous, with slightly prominent main nerves, the smaller ones less conspicuous; midrib and 8–9 pairs of secondary nerves prominent beneath, the latter subascendent, curving and anastomosing near the margin, smaller veins prominulous and reticulate, often with glandspots on the nerves at the middle.

Inflorescence cymose-paniculate, dichotomous, ending the branchlets or in the axils of the upper leaves; peduncle strong, sparingly puberulous, the branchlets rather thick and densely hirtellous. Pedicels thick, about 2 mm. long, densely hirtulo-pubescent. Bracts ovate, about 1.5 mm. long, soon deciduous. Calyx about 2 mm. high, pubescent, with suborbicular, ciliate lobes. Petals white, linear-oblong, 10–13 mm. long, 2.5–3 mm. wide, densely hirtulo-pubescent outside with spreading or retrorse hairs, margin glabrous, estivation contorted. Stamens more than 100; 2–3 seriate, united at base in a cup; the filaments glabrous, unequal, 6–9 mm. long. Anthers ovate-lanceolate, 0.8–0.9 mm. long, with fleshy, lanceolate connective and 4 elliptic, basilar lobes. Disk annular, girdling the ovary, glabrous, 1 mm. high. Ovary subglobose, 2 mm. high, densely hirsute-villose, with 5 biovulate cells. Style thick, erect, pilose only at base, 4–6 mm. long. Stigmas obtuse. Drupe ovoid, rounded at base, obtuse at apex, densely tomentous, about 2.2 cm. long, 1.6 cm. diameter.

V. obovata is a small tree at present only known from the States of Minas Geraes and Bahia in Brazil.

BRAZIL: MINAS GERAES: Diamond Dist., common on the Serra Mendanha, small tree, *Gardner* 4452 (BM). Estrada de Bom Gosto a Olivença; arvore, 15–III–1943, *Fróes* 19933 (NY, IAN, US). Carrasco-Chapadão, Municipio de Diamantina, muito frequente; flores alvas, arbusto 2 m., 29–IV–1942, *Mendes Magalhães* 2117 (IAN). “Minas Geraes,” *St. Hilaire* B 1705 (P, holotype); photo F.M. 35175. Minas Geraes, Catal B, *St. Hilaire* 1984 bis (P). Biribiry, arbuste fleur blanc jaunâtre, 22–III–1892, *Glaziou* 18963 (P, US); photo F.M. 12590 of *Gardner* 4452. “Habitat in alpestribus districtus adaman-tini prope Tejuco, etc., Provinciae Min. General. Dr. Martius Iter Brasil.,” Jul., *Martius* s.n. (M, holotype). Minas Gerais, Dr. Martius Iter Brasil. Observ. 1274, *Martius* s.n. (M, 3 sheets). Brasilia in altis Serra do Frio, Provinciae Minarum Generalium, Observ. 1274 conf. *Hirtella polyandra* Kunth, *Martius* s.n. (M). Brasilia in alpestribus Provinciae Minarum Generalium, Dr. Martius Iter Brasil., *Martius* s.n. (M, isotypes, 2 sheets). BAHIA: Campos casa Pedra, 27–VII–1914, *Luetzelburg* 40 (M). Jussieu quoted for *V. obovata* the following location, probably based on St. Hilaire’s collections: “Nascitur prope vicum Curumatahy in parte deserta occidentalique Provinciae Minas Geraes quam vocant Certao.”

3. *Vantanea barbourii* Standl. Trop. Woods 75:5. 1943.—Barbour, *ibid.*: 7–8. 1943.—Record, *ibid.*, 77:8–9. 1944.—Allen, The rain forests of Golfo Dulce 351, fig. 20. 1956. FIGURE 9, f–h

Type: *Dayton & Barbour* 3129, Costa Rica, Cartago.

Large tree with angular, somewhat lenticellate, glabrous branchlets. Leaves coriaceous, firm, glabrous. Petioles 6–10 mm. long, flat above, thickened at base. Blades entire elliptic or oblong-elliptic, attenuate at both ends, cuneate base, obtuse but sometimes rotundate or even emarginate apex, 5–12 cm. long, 2.4–6 cm. wide; above brownish-green, lustrous, with midrib and secondary nerves flat and conspicuous, the smaller veins little visible or obsolete; pale-brownish with prominent midrib beneath, the 7–9 lateral nerves on each side, prominent, ascendent, curved and connected at the ends, the lesser veins prominulous, loosely reticulate.



FIGURE 9.—a, *Vantanea occidentalis*, $\times \frac{1}{3}$ (Cuatr. 19937); b, *Vantanea occidentalis*, bud, $\times 1\frac{2}{3}$; c, *Vantanea paraensis*, $\times \frac{1}{3}$ (Ducke 752); d, *Vantanea paraensis*, bud, $\times 1\frac{2}{3}$ (Ducke 17782); e, *Vantanea paraensis*, petal, $\times 1\frac{2}{3}$ (Ducke 17782); f, *Vantanea barbourii*, $\times \frac{1}{3}$ (Dayton & Barbour 3129); g, *Vantanea barbourii*, bud, $\times 1\frac{2}{3}$; h, *Vantanea barbourii*, petal, $\times 1\frac{2}{3}$.

Inflorescence axillary subterminal, paniculate-cymose, leafy, as long as the leaves, the peduncle strong, glabrous or subglabrous, the branchlets angled, dichotomo-furcate, shortly hirtellous. Bracts caducous. Pedicels 1–2 mm. long, minutely puberulous. Calyx 1–1.5 mm. high, slightly puberulous, deeply lobate, with rounded ciliate lobes. Petals white, oblong, subacute, attenuate towards the apex, glabrous inside, adpressed retrorse-pubescent outside, about 7 mm. long and 2.5 mm. wide. Stamens 50–60, glabrous, the filaments 5–7 mm. long, complanate, united at base. Anthers ovate-lanceolate, about 0.8 mm. long, with 4 small, ellipsoid lobes, the connective thick, acuminate-lanceolate, twice as long as the lobes. Disk thick, glabrous, 1 mm. high; margin short-denticulate. Ovary ovoid, 1.5–2 mm. high, densely tomentose-hirsute, 5-loculate, cells biovulate. Style rigid, glabrous, about 4 mm. long. Drupe ovoid-oblong, smooth, obtuse at the base, attenuate at the apex, 2.8–3 cm. long, 1.8–2 cm. broad. Endocarp ellipsoid-ovoid, oblong, about 2.7 cm. long, 1.6 cm. broad, obtuse at both ends; the valves 5, oblong, obtuse at apex, about 1.8 cm. long, 4–5 mm. wide.

Of *V. barbourii*, Paul Allen gives a good illustration and writes the following first hand data and observations: “*Ira chiricana* or *Nispero*. Tall forest trees, 90–120 ft. in height and up to 5 ft. in diameter above the basal buttresses, with alternate, short-petiolate, leathery leaves, the oblong-elliptic blades 3.5 in. in length, with rounded or emarginate apices and cuneate bases. The trees are completely deciduous for a brief period at about the end of the heavy rains in November or December. The small white flowers are produced in June, and again from about November until January in dense terminal or subterminal corymbs, followed by ellipsoidal fruits about 1 in. in length. The seeds have a very distinctive appearance, and are frequently seen on the forest floor. The strong, reddish-brown wood is fairly hard and heavy, and is reported to be very durable, having been used for bridge timbers on the Pan-American highway. Locally very common on forested hillsides up to about 2,500 ft. in elevation. Golfo Dulce, without definite locality, H. J. Marks, s.n. (Yale School of Forestry 16822), Esquinas Forest, 250 ft., *Allen* 6546, Hills near Palmar Sur, 200 ft., *Allen* 6681.”

Barbour states: “The range of *Ira Chiricana*, so far as is now known, is confined to a relatively small area on the rolling hills near San Isidro, at elevations from 700 to 800 meters above sea level . . . [It] . . . has a thin brownish gray bark with longitudinal fissures. It is usually buttressed at the base, above which it has a good timber form. Specimens 36 inches or more in diameter with 40 feet or more of clear length, are not uncommon. Its fairly hard and heavy reddish brown wood has a good local reputation for strength and

durability and is being used for bridge timbers on the Inter-American Highway, which traverses its range."

COSTA RICA: SAN JOSÉ: 1 mile north of San Isidro del General, $\frac{1}{2}$ mile west of Pan-American Highway, right of way, alt. 2,500 ft., rain forest, grows in patches, tree 70 ft. high, DBH 12 in., size up to 100 ft., usable length 40 ft., strongest wood in this locality used for heavy construction, pits in scalariform arrangement bark brownish gray with longitudinal fissures, 11-VI-1943, "ira chiricana," *Dayton & Barbour* 3129 (US, holotype; F, isotype). CARTAGO: 2 km. south of Rio Hermosa, about 8 km. from San Isidro del General, alt. 2,100 ft., mixed virgin forest, tree 75 ft. high, DBH 16 in., 6-IX-1943, "níspero," "ira chiricana," *Barbour* 1018 (F, Y).

4. *Vantanea occidentalis* Cuatr. Trop. Woods 96:40. 1950.

FIGURES 1; 6, *j-l*; 9, *a-b*

Type: *Cuatrecasas* 19937, Colombia, Valle, Buenaventura.

Large tree; branchlets green, cinnamon-brown when dry, lustrous, glabrous. Petioles 1–5 mm. long, robust, sulcate above, thickened at base. Leaf blades coriaceous, entire, cinnamomeous when dry, elliptic, obovate-elliptic or oblong-elliptic, cuneate at base, abruptly attenuate, obtuse or shortly acuminate at apex, 7–16 cm. long, 2.5–8.5 cm. broad; green above, lustrous, with well-marked midrib, the secondary ones immersed, obsolete; with thick and prominent midrib beneath, the 8–10 secondary nerves on each side prominent, ascendent, near the margin arched and united, the minor veins loosely reticulate, slightly prominulous.

Inflorescences at the end of the branchlets paniculate, shorter than the upper leaves, many-flowered; branchlets dichotomously articulate, shortly pubescent; the bracts caducous, not seen by the author. Pedicels thick, puberulous, 1–2.5 mm. long. Sepals orbicular, subcoriaceous, glabrous or subglabrous, pale greenish, 6–7 mm. long with a single gland outside. Petals subcoriaceous, oblong, rather obtuse, 9 mm. long, 3 mm. wide, glabrous, outside greenish-white, inside white. Stamens numerous (about 80); filaments unequal, about 8 mm. long, linear, rather thick, acute at apex, white, glabrous, united at base. Anthers small, ovate-lanceolate, the connective thick at base, acute at apex. Disk cupular, 1 mm. high, striate, minutely dentate, glabrous. Ovary 3–4 mm. high, very hirsute, with 5 or 6 biovulate cells. Styles filiform, 5 mm. long. Drupe oblong-ovoid-ellipsoid, narrowed at both ends, about 3.5 cm. long and 1.8 cm. broad. Endocarp woody, one-celled, about 3 cm. long and 1.5–1.7 cm. thick, ellipsoid-oblong, attenuate and subacute at both ends; surface rather smooth, with 5 broad ribs alternating with 5 oblong, 2-cm. long and 5-mm. wide valves, only one of them removable. One oblong seed in the single remaining cavity developed, about 2 cm. long.

V. occidentalis is a rain forest hardwood tree with a distribution restricted to the western Colombian coast and Chocó region.

COLOMBIA: VALLE: Bahía de Buenaventura (Costa del Pacífico), Quebrada de San Joaquín, 0–10 m. alt.; árbol grande; hoja coriácea, flexible, verde brillante haz; capullos verde claros, pétalos blanco-verdosos por fuera, blancos por dentro, filamentos blancos; drupa verde, dura, ovoideo-aguzada, 3 cm. long, 22-II-1946, *Cuatrecasas* 19937 (F, holotype; G, VALLE, US, isotypes). Buenaventura, 1945, *Patiño* 12 (F, US, paratypes). Chocó: Quibdó, alt. 40 m., III-1958, "chanó," only fruits from the ground, *Ramos & Patiño* s.n. (US).

5. *Vantanea paraensis* Ducke, Arch. Jard. Bot. Rio Janeiro 4:99. 1925.—
Arch. Inst. Biol. Veget. Rio Janeiro, 4:30, 31. 1937.

FIGURES 6,*a-c*; 9,*c-e*

Type: *Ducke* 17782, Brazil, Pará, Rio Tapajoz.

Large tree; branchlets subterete, glabrous, sparsely lenticellate. Leaves rigid, thick-coriaceous, glabrous. Petioles 10–15 mm. long, semiterete, subsulcate above, thickened at base. Blades entire, obovate-elliptic, cuneate at base, broadly obtuse or subrounded and occasionally emarginate at apex, 7–12 cm. long, 3–6.5 cm. wide; obscurely yellowish-green above with prominulous midrib and less visible secondary nerves; pale with thick midrib beneath, the secondary nerves 8–10 on each side, prominent, ascending at some distance from the margin, thinner and arcuately connected, the lesser veins prominulous and loosely reticulate.

Inflorescence cymose-paniculate, ending the branchlets or axillary in the upper leaves, corymbiform, dichotomous at summit, rather smaller than the leaves; peduncle strong, ribbed, slightly hirtellous-puberulous; branchlets angled, hirtellous-puberulous. Bracts soon deciduous. Pedicels thick, subterete, minutely puberulous or glabrous. Calyx 5-lobate, about 0.5 mm. high and 1.5 mm. in diameter, with rounded, outwardly glabrous lobes, margin minutely ciliate. Petals white, thickish, oblong, subacute, glabrous, 6–8 mm. long, 2–2.5 mm. wide above the base, estivation contorted. Stamens about 50, the filaments glabrous, flexuous, complanate below, shortly united at base; the anthers ovate-lanceolate, about 0.9 mm. long with 4 ellipsoid lobes and fleshy, lanceolate, elongate connective. Disk thick, annular, glabrous, about 1 mm. high with dentate margin. Style 3.5–5 mm. long, only pilose at base, thick but attenuate toward the apex. Ovary ovoid, about 2 mm. high, furrowed, densely and shortly velvety-tomentose, 5-celled, the cells biovulate. Stigma obtuse. Drupe oblong-ellipsoid about 5–5.3×2.8–3 cm.; exocarp coriaceous when dry, about 2 mm. thick, glabrous or subglabrous; endocarp woody, oblong, obtuse at base, thick above, narrowed and acute at apex or apiculate, 4.6 cm. long, 2.5 cm. broad, the surface slightly rugose; the valves 7, linear-oblong, obtuse at apex, 3–3.5 cm. long, about 5 mm. broad.

V. paraensis is a Brazilian species, known only from the regions of Manaus and Rio Tapajoz.

BRAZIL: AMAZONAS: Manaus, silva non inundabili ultra flores; arbor magna floribus albis, 12-VII-1941, *Ducke* 752 (IAN, MG, US). Manaossilva terris altis circa rivum Mindú superiorem; arbor magna, floribus albis suaveolentibus, 22-X-1929, *Ducke* 23430 (P, S, U, US). Lago de Badajoz, rio Capitari, terra firme, alta, floresta alta arvore 25 m., flores brancas, 29-VIII-1950, *Fröes* 26428 (IAN, US). PARÁ: Rio Tapajoz, circa cataractas infimas loco Bella Vista, silva non inundabili, arbor magna floribus albis, 24-IX-1922, *Ducke* 17782 (US, S, U, isotypes), photo F.M. 12591 from Berlin.

6. *Vantanea celativenia* (Standl.) Cuatr., comb. nov.

FIGURES 6,d-f; 10,a-b

Licania celativenia Standl. Field Mus. Bot. 17:254. 1937.

Type: *Krukoff* 7182, Brazil, Amazonas, Rio Madeira.

The vegetative parts of this species agree completely with *V. paraensis*, at least for the specimens now available. But the fruit of the type of Standley's species are so different that they define



FIGURE 10.—a-b, *Vantanea celativenia*, $\times \frac{1}{2}$ (*Krukoff* 7182); c, *Vantanea compacta*, $\times \frac{1}{2}$ (*Blanchet* 3362); d, *Vantanea compacta* bud, $\times 1\frac{1}{2}$; e, *Vantanea compacta*, petal, $\times 1\frac{1}{2}$; f, *Vantanea micrantha*, $\times \frac{1}{2}$ (*Ducke* 751); g, *Vantanea minor*, $\times \frac{1}{2}$ (*Tamayo* 3123).

another species. The flowers, which are lacking, probably will provide complementary characterization when found.

Drupe ovoid-ellipsoid, about 3 cm. long and 1.6–1.7 cm. broad, rounded at the base, acute at apex. Exocarp thin (about 0.5 mm. thick when dry), minutely papillose and sparsely pilose. Endocarp woody, ovoid-ellipsoid, more or less oblong, rounded at base, acute or shortly apiculate at apex, 2.8–3 cm. long, about 1.6 cm. broad, marked by 5 broad ribs alternating with 5 oblong, appressed valves, 2.2 cm. long, 4 mm. wide.

The distribution of *V. celativenia* is restricted to the Município de Humaytá in the State of Amazonas, Brazil.

BRAZIL: AMAZONAS: Basin Rio Madeira, Município de Humaytá, on plateau between Rio Livramento and Rio Ipixuna; tree 110 ft. high, on campinarana, 7-18-IX-1934, *Krukoff* 7182 (US, NY, S, U, isotype of *Licania celativenia*). Município of Humaytá, near Tres Casas, on lower terra firma, trees 120 ft. high, 14-IX-11-X-1934, *Krukoff* 6371 (A, BM, NY, S, U, US).

7. *Vantanea micrantha* Ducke, Arch Inst. Biol. Veget. Rio Janeiro 4:30. 1938.

FIGURES 5,*m-n*; 7,*e-f*; 10,*f*

Type: *Ducke* 30135, Brazil, Amazonas, Manaus.

Large tree with slender, gray, almost smooth, sparsely lenticellate branchlets, glabrous or the youngest ones puberulous. Leaves thin-coriaceous, glabrous. Petioles 3–6 mm. long, sulcate above. Blades entire, elliptic-oblong or elliptic-lanceolate, broad near the base, abruptly narrowed and tapering to the petiole, narrowed-acuminate or cuspidate at apex, 5–12 cm. long, 2–5 cm. broad; green-olivaceous and with prominulous midrib above, the secondary nerves and veins very thin; lighter and with prominent midrib beneath, the secondary nerves 10–12 each side, slender, curved-ascending, prominulous, the veins reticulate, prominulous; bearing a few seriate glands at the middle.

Inflorescences cymose-paniculate, axillary and terminal, much shorter than the leaves, the peduncle and branches minutely hirtellous or papillose. Bracts early deciduous, ovate-lanceolate, about 1.2 mm. long. Pedicels thick, 0.5 mm. long. Calyx 0.6–0.7 mm. high, subcupular, slightly 5-lobate, the lobes very obtuse, sparsely papillose outside, minutely ciliolate at margin. Petals white, glabrous, oblong, about 5 mm. long, 1.5 mm. broad at base, the estivation contorted. Stamens about 50, glabrous, the filaments slender, flexuous, unequal, 2.5–4 mm. long, united at base. Anthers ovate-lanceolate, 0.6–0.7 mm. long, with 4 elliptic lobes, the connective fleshy, elongate, acute or subacute. Disk glabrous, girdling the ovary, about 1.2 mm. high, the upper half laciniate. Ovary ovoid, glabrous, striate, 1 mm. high, with 5 biovulate cells. Styles rigid, glabrous, about 4 mm. long. Drupe ellipsoid, about $2-2.5 \times 1.4-2.2$ cm., yellowish. Endocarp

ellipsoid-obtuse, woody, strongly costate-corrugate, somewhat resembling the cotyledons of a walnut, about 2×1.6 cm. Exocarp thin, oleaginous, sweetish, aromatic.

Characterized by its small, white flowers and small fruit, *V. micrantha* is only known from the floodless lands of the Manaos region in Brazil.

BRAZIL: AMAZONAS: Manaos, silva terris altis circa cataractas fluvii Taruma; arbor magna floribus albis, 6–VIII–1937, *Ducke* 30135 (US, P, S, U, isotypes). Manoas, silva non inundabili ultra Coloniam João Alfredo, arbor magna floribus albis, 7–XIII–1941, *Ducke* 751 (GH, MG, IAN, NY, US).

8. *Vantanea minor* Benth. in Hook. Journ. Bot. Kew Misc. 5:99. 1853.—Urb. in Mart. Fl. Bras. 12(2):452. 1877. FIGURES 5,f–l; 7,g–h; 10,g

Type: *Schomburgk* 1552, British Guiana.

Medium-size tree with subterete, smooth, glabrous or minutely and sparsely puberulous branchlets. Leaves coriaceous, rigid, glabrous. Petioles very short, 1–2 mm. long. Blades entire, obovate or elliptic-obovate, acute or obtusely cuneate at the base, rounded or very obtuse at the apex, sometimes emarginate, 3–8.5 cm. long, 1.6–4.5 cm. broad; above lustrous, green, midrib slightly prominulous, minor veins almost obsolete; cupreous and with prominent midrib beneath; 13–15 secondary nerves on each side, filiform, prominulous, united near margin, minor veins loosely reticulate, slightly prominulous; bearing a few seriate glands on each side of midrib.

Inflorescences terminal and axillary-terminal, cymose-paniculate, with furrowed and minutely puberulous branches. Pedicels thick, slightly and minutely puberulous, 1.5–2.5 mm. long. Calyx about 2 mm. high, lobes thick, subrotundate, glabrous outside, margin ciliate. Petals linear-oblong, thickish, white, glabrous, 12–14 mm. long, 2 mm. broad; estivation contorted. Stamens more than 100, pluriseriate, 9–12 mm. long, glabrous, united in a 3–4 mm. high tube at base, free part of filaments filiform. Anthers about 0.6 mm. long with 4 ellipsoid lobes, the connective thick and obtuse. Disk tubular, thick with toothed margin, glabrous, 1.2 mm. high, girdling the ovary. Ovary ovate, glabrous, about 2 mm. high, with 5 biovulate cells, the ovules superposed. Styles flexuous, about 12 mm. long, glabrous. Stigma obtuse. Drupe 3.5–5 cm. long, 2.2–3 cm. broad, oblong-ellipsoid or ovoid-ellipsoid, rounded at base, obtuse at apex. Exocarp coriaceous when dry, resinous, reddish-brown, rather smooth, glabrous, 2 mm. thick. Endocarp woody, ellipsoid, broadly rounded at base, abruptly apiculate or obtuse at apex, 3–4 cm. long, 2–3 cm. broad, strongly anfractuose-rugose, inside slightly cavernous; opercula 5, oblong, obtuse at the apex, about 22 mm. long, 5 mm. broad (*Bernardi* 2613) alternating with 5 small foveolae at the top. In a

sectioned specimen (2613) 4 oblong monospermous cavities about 22 mm. long, 3 mm. thick can be seen.

For the description of the fruits, which were unknown before, I used the Cardona (2362) and Bernardi specimens. Bernardi's endocarps are more obtuse at the top than those of the Cardona specimens, but I have no doubt about their being conspecific and about their identity with Benthams species.

V. minor is endemic in the Guiana region which is called Gran Sabana in Venezuela and nearby British Guiana.

VENEZUELA: BOLIVAR: Sabana de Icaburu, entre la reducida faja de vegetación leñosa a lo largo del río, aguas negras, alt. 450–850 m.; árbol 5 m., flores blancas, grandes, frutos grandes monospermos, 22–XII–1955, *Bernardi* 2613 (VEN). Gran Sabana, selvas de galería del río Urari; arbusto, y a veces árbol muy frondoso en la selva de galería, en matorrales de la serranía es achaparrado y menos frondoso, III–1946, *Tamayo* 3123 (US). Camino del Río Tirica que sale a la Gran Sabana, 900 m. alt., árbol 15 m., X–1947, *Cardona* 2362 (US). Río Caroní, sitios pedregosos en las orillas del Uaiparu, afluente del Icabaru, 500 m. alt., árbol 10 m., 27–X–1946, *Cardona* 1912 (US, VEN). Río Cuquenán al sur del Roraima; Blueten weisslich, am Quewewode, II–1910, *Ule* 8801 (MG,K).

BRITISH GUIANA: No locality, *Schomburgk* 1552, photo F.M. 12589 of type in Berlin.

9. *Vantanea peruviana* Macbr. *Candollea*, 5: 371. 1934.—Flora of Peru, Field Mus. Bot. 13:632. 1949. FIGURE 11, c–e

Type: *Klug* 1130, Peru, Loreto.

Medium-size tree with reddish-brown, lenticellate, glabrous branchlets. Leaves rigid-coriaceous, glabrous. Petioles 3–4 mm. long, thickened at base. Blades entire, obovate or obovate-elliptic, cuneate at base and decurrent on the petiole, rounded, truncate or even retuse

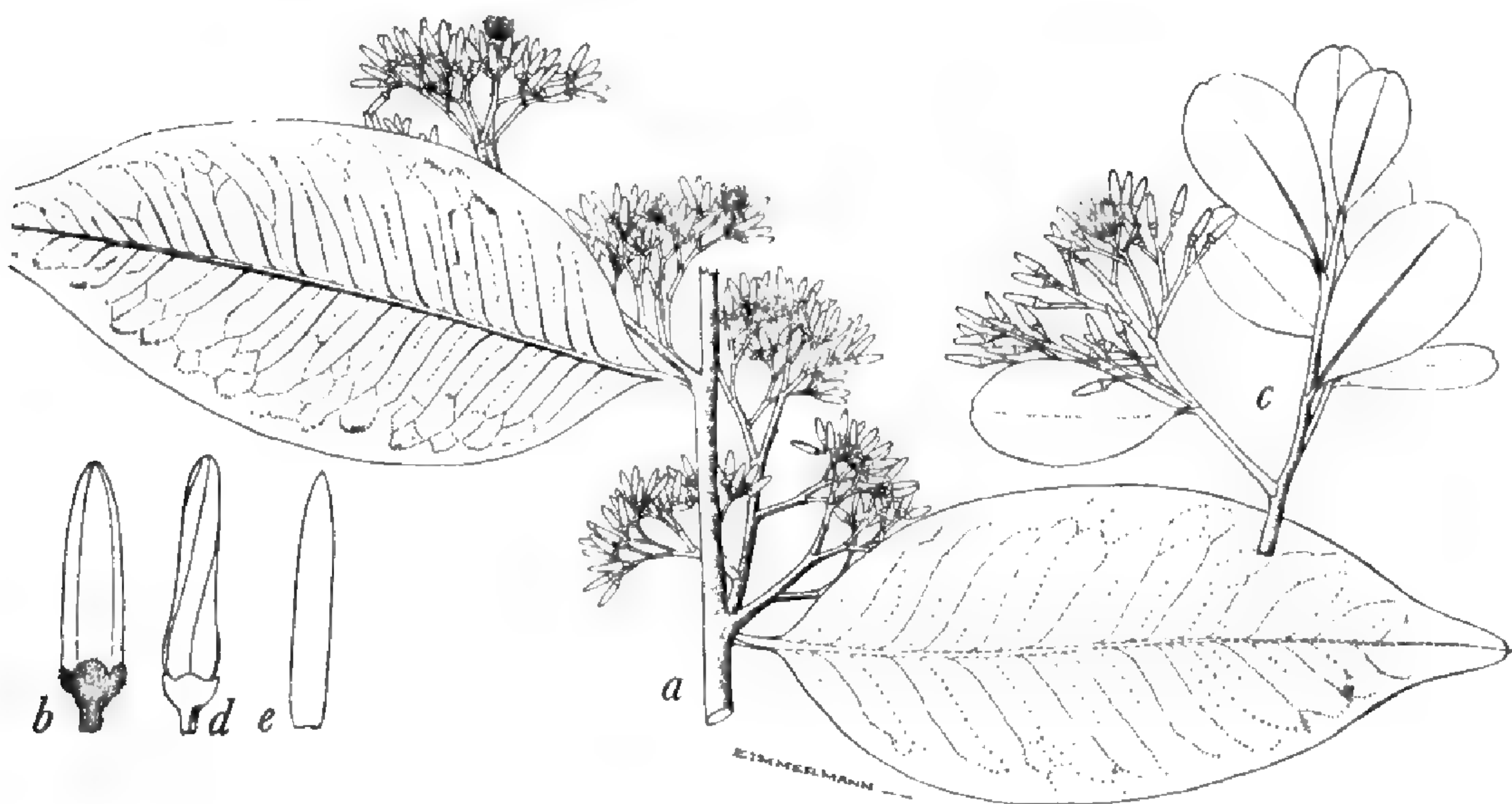


FIGURE 11.—a, *Vantanea macrocarpa*, $\times \frac{1}{2}$ (*Ducke* 30133); b, *Vantanea macrocarpa*, bud, $\times 1\frac{2}{3}$; c, *Vantanea peruviana*, $\times \frac{1}{2}$ (*Klug* 1130); d, *Vantanea peruviana*, bud, $\times 1\frac{2}{3}$ (*Klug* 1091); e, *Vantanea peruviana*, petal, $\times 1\frac{2}{3}$ (*Klug* 1091).

at the apex, 3–8 cm. long, 1.2–4.5 cm. broad; greenish and lustrous above with marked midrib and almost obsolete veins; brown when dry beneath, with prominent midrib; secondary nerves 10–12 on both sides, very slender, almost obsolete, arched and united near the margin, the lesser veins inconspicuous; bearing a few minute glands spread at the middle.

Inflorescences in axils of uppermost leaves, forming cymose corymbiform pseudoterminal panicle; peduncle and branchlets robust, angled, hirtello-puberulous. Bracts deciduous. Pedicels thick, glabrous or subglabrous, 1–1.5 mm. long. Calyx cupular, thick, about 1.2 mm. high, 5-lobate, lobes subrounded, glabrous outside, the margin minutely ciliolate. Petals white, thickish, linear, acutish, glabrous, about 11 mm. long, 1.5–1.8 mm. broad. Stamens about 70, glabrous, the filaments slender, flexuous, 7–10 mm. long, united in a tube 1–1.5 mm. high. Anthers ovate, 0.6 mm. long, with 4 ellipsoid lobes, the connective fleshy, oblong, obtuse. Disk tubular, glabrous, with toothed margin, girdling the ovary, 1.5 mm. high. Ovary ellipsoid, glabrous, 1.5 mm. long, with 5 biovulate cells. Styles erect, glabrous, about 7 mm. long. Fruit unknown.

This species is only known from the type locality in Amazonian Peru.

PERU: LORETO: Mishuyacu, near Iquitos, alt. 100 m., forest, tree 10 m., flowers white, IV-1930, *Klug* 1130 (isotype, US); tree 12 m. high, flowers white, II-III-1930, *Klug* 1091 (US).

10. *Vantanea compacta* (Schnizl.) Cuatr., comb. nov.

FIGURES 7,*a-b*; 10,*c-e*; PLATE 1

Humirium compactum Schnizl. Abbild. Nat. Fam. 3:Ordo 222, pl. 222. 1843–1870.

Humirium contractum Moric. Msc. Schnizl. in Urb., Bot. Jahrb. 15, Beibl. 34:3. 1892.

Vantanea contracta Urb., ibid.

Vantanea panniculata Urb. in Mart. Fl. Bras. 12(2):450, pl. 96. 1877.

Type: *Blanchet* 3362, 3305, Brazil, Bahia.

Medium or large tree; branchlets slender, lustrous, densely lenticellate, glabrous or slightly puberulous. Leaves small, coriaceous, moderately rigid, glabrous or sometimes sparsely and appressed puberulous. Petioles 3–6 mm. long, thickened at base. Blades entire, oblanceolate or lanceolate-elliptic, shortly or longly cuneate at base, attenuate, acuminate or long-cuspidate at apex, callous-thickened and slightly revolute at margin, 3.5–7 (–9) cm. long, 1.3–2.5 (–4) cm. broad; shining above, midrib more or less marked, other nerves almost inconspicuous; beneath with prominent midrib, 8–9 secondary nerves slightly prominulous on each side, lesser veins loose and thin.

Inflorescence cymose-paniculate, axillary, small, equaling the leaves or shorter, axis and branchlets angled, minutely pubescent-hirtellous. Bracts deciduous. Pedicels thick, minutely hirtellous, 0.5–1.5 mm. long. Calyx cupular, 1 mm. high, scarcely puberulous, 5-lobate; lobes subrotundate (0.3–0.5 mm. long), with minutely ciliate margin. Petals white, linear-oblong, subobtuse, glabrous, 4–5(–8) mm. long, 1.5–1.8 mm. wide. Stamens about 50–60, filaments slender, flexuous, 1.5–4(–7) mm. long, united in a 0.6 mm. high ring. Anthers ellipsoid, about 0.7–0.9 mm. long, with 4 oblong, apiculate lobes about 0.5–0.6 mm. long, the connective with acute, 0.3–0.4 mm. long tip. Disk annular, girdling the ovary, glabrous, 1 mm. high with strongly denticulate margin. Ovary ovoid, 1.5 mm. high, minutely velvety-sericeous, with 5 biovulate cells. Style 2–3 mm. long, erect, thickish, pubescent on the lower half. Stigma obtuse. Drupe oblong-obovate-ellipsoid, rounded at apex, attenuate at base, 2.4–2.8 cm. long, 1.5–1.8 cm. diameter; the exocarp smooth, 1–1.5 mm. thick, coriaceous, brittle when dry. Endocarp woody, oblong, ellipsoid, obtuse at apex, slightly narrowed at base, up to 2.5×1.4 cm.; the surface rugose with 5 slight furrows toward the base and 5 longitudinal, oblong, germinal valves 1.8–2 cm. long, slightly conspicuous. Only one oblong seed in the single cavity observed. The drupe may be smaller and globose-ovoid in a subspecies.

Usually the leaves are completely glabrous. Only in one specimen (*Blanchet* 85) have I seen very sparse, minute, appressed hairs beneath. The *Ducke* 1513 collection, which is preserved at the Museu Goeldi, has some larger leaves (up to 9×4 cm.) than the regular type; nevertheless, this collection agrees with the other characters of *V. compacta*, despite the smaller leaves of the specimens. *Blanchet* 85 in Paris with regular, small leaves also has one large (8.5×4 cm.) leaf. *Ducke* 1513 is the only collection of the species that I have seen with fruit and is the basis for this part of the description.

V. compacta is restricted to the eastern States of Brazil, from Ceará to Santa Catarina; however, the Pearce collections indicate the presence of a new subspecies on the eastern slopes of the Bolivian Andes.

The specific epithet published by Schnizlein, is “compactum” and is the correct and valid name for the species; “compactum” is used several times in the detailed explanation of plate 222 of Schnizlein, the explanation amounting to the original description. Urban erroneously quoted “*Humirium contractum*” as the name published by Schnizlein—a herbarium name presumably handwritten by Moricand on a Martius herbarium sheet (which is the type). But for some unknown reason, when Schnizlein published his very fine drawing and analysis of the species, he used the name “compactum,” and it therefore has priority.

The specimens used by Schnizlein were reportedly from the Martius Herbarium ("Saemmtliche Figuren nach Exemplaren aus v. Martius Herbarium"), but this species is not among the humiriaceous collections received from Munich. Martius probably did not collect the species himself, and the specimens that he used were those collected by Blanchet. The type of *V. panniculata*, *Blanchet* 3305, must be the first collection cited by him. The type of *V. contracta* (Morici) Urban is *Blanchet* 3362, which is in the Paris Herbarium and was originally labeled with name and analysis by Moricand and cited by Urban. I think that this same specimen (*Blanchet* 3362) ought to be considered the type of *Humirium compactum* Schniz.

10a(1). *Vantanea compacta* subsp. *compacta* var. *compacta*

BRAZIL: BAHIA: Jacobina, Igreja Velha, *Blanchet* 3362 (holotype, P; isotypes, GA, NY); *Blanchet* 3805 (holotype of *V. panniculata*, P; isotype, NY). Camandica, *Blanchet* 3837 (P); *Blanchet* 85 (P). CEARÁ: Guaramiranga, mata das collinas ao redor da ville; arbor pequena, 8-VIII-1908, frutos, *Ducke* 1513 (MG). RIO DE JANEIRO: Petrópolis ao Retiro, 5-III-1880, "Maçaranduba de folha miuda," *Glaziov* 11829 (P); Corcovado, 4-II-1880, *Glaziov* 11828 (GH, BM, IAN, NY, P). Alto Macahé, 7-IV-1891, arbrisseau, *Glaziov* 18182 (P, US). SÃO PAULO: Jardim Botânico, "Aroeirana," 10-X-1933, 17-III-1932, *Hoehne* 29281 (A, GH, NY, S, P). SANTA CATARINA: Mata da Azambuja, Brusque, "guaraparín," 23-II-1950, *Klein* 37b (S, US). Brusque, arvore 20 m., flor verde amarelada, "guaraparín," 23-II-1950, *Reitz* 3353 (S, US). Horto Florestal INP, Ibirama, 300 m. alt., mata, arvore 20 m. flor branca, "guaraparín," 1-III-1954, *Reitz & Klein* 1589 (US, S, U). Morro da Fazenda, Itajaí, 50-350 m., mata, "guaraparín," arvore 20 m., 14-V-1954, *Reitz & Klein*, 1836 (US); 4-III-1954, *Reitz & Klein* 1730 (US); arvore, flor branco amarelada, 18-III-1954, *Reitz & Klein* 1744 (US, U, S).

10a(2). *Vantanea compacta* subsp. *compacta* var. *grandiflora* (Urb.), Cuatr., comb. nov.

Vantanea contracta var. *grandiflora* Urb. Bot. Jahrb. Engler, Beibl. 34:3. 1893.

Type: *Glaziov* 16723, Brazil, Rio de Janeiro.

Flowers larger than ordinary; petals 7-8 mm. long; stamens about 80. Leaves puberulous with minute, sparse, appressed hairs beneath. Inflorescences pauciflorous.

BRAZIL: RIO DE JANEIRO: Alto Macahé, 5-III-1888, *Glaziov* 16723 (isotypes US, P). Alto Macahé, arbor, 11-III-1891, *Glaziov* 18181 (paratype P). Rio de Janeiro, III-1891, *Glaziov* 14640 (US).

10b. *Vantanea compacta* subsp. *microcarpa* Cuatr., subsp. nov. PLATE 2

Arbor 10-20 m. alta ramis terminalibus tenuibus glabris. Folia tenuiter coriacea flexibilia oblongo-elliptica basi longe angustata cuneata apice paulo attenuata obtusiuscula. Petiolus 4-6 mm. longus. Lamina 5-8 cm. longa 2-4.5 cm. lata costa praecipue subtus notata nervis secundariis venulisque leviter conspicuis. Calyx cupularis sepalis subrotundatis dimidia inferiore parte connatis glaberrimis 1 mm. longis. Petala crassiuscula oblonga sursum angustata subacuta

4–5 mm. longa 1.5–1.8 mm. lata, aestivatione contorta. Stamina circa 58 glabra epapillosa filamentis flexuosis 1.5–3.4 mm. longa tantum basi coalita. Antherae ovoideo-ellipsoideae circa 0.9 mm. longa, apiculo 0.3–0.4 mm. longo acuto incluso. Discus annularis argute dentatus 0.8–1 mm. altus. Ovarium ovoideum circa 1.5 mm. altum minute velutino-sericeum. Stylus 2–2.5 mm. longus glaber. Stigma anguste capitatum breviter 5-lobatum. Drupa globoso-ovoidea 1.6–1.8 cm. longa 1.4–1.6 cm. lata basi rotundata apice obtusissima vel subrotundata, exocarpio laevi in sicco 0.6–1 mm. crasso. Endocarpium subgloboso-ovoideum circa 1.7– \times 1.4 cm. rugulosum basi rotundatum apice obtusum, 5 valvis longitudinalibus obovato-oblongis circa 1.4 cm. longis basim versus argute exculptis instructum; sectione 10 radiatum raro 5 cavitatis saepe tantum 1–2 cavitatis seminiferis monospermis evolutis.

Type in the Kew Herbarium, tree 70–80 ft. high, collected at “Chailla” (probably Challa), Bolivia, May 1866, by R. Pearce. Paratype in the Kew Herbarium collected at Moro, Yungas, Bolivia, January 1866, by R. Pearce; isoparatype also in British Museum.

This subspecies is only known from the Bolivian type localities.

BOLIVIA: “Chailla” according to the collector, but probably “Challa”; tree 70–80 ft.; V-1866, *Pearce* s.n. (type, K). Yungas, Moro, alt. 500–600 ft., tree 40–50 ft., I-1866, *Pearce* s.n. (paratype, K, BM).

11. *Vantanea macrocarpa* Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 1:205. 1935.—Trop. Woods 43:20. 1935. FIGURES 11,*a-b*; 12

Type: *Ducke* 20427, Brazil, Amazonas, Manaus.

Large tree with glabrous greenish brown, densely lenticellate branchlets. Leaves thick-coriaceous, glabrous. Petioles 8–12 mm. long, thick, sulcate above. Blades ovate-oblong or elliptic-oblong, rounded or obtuse at base and decurrent upon the petiole, attenuate and obtusely acuminate at apex, entire and thickened at the margin, 11–20 cm. long, 5–10 cm. broad, both sides brownish when dry;

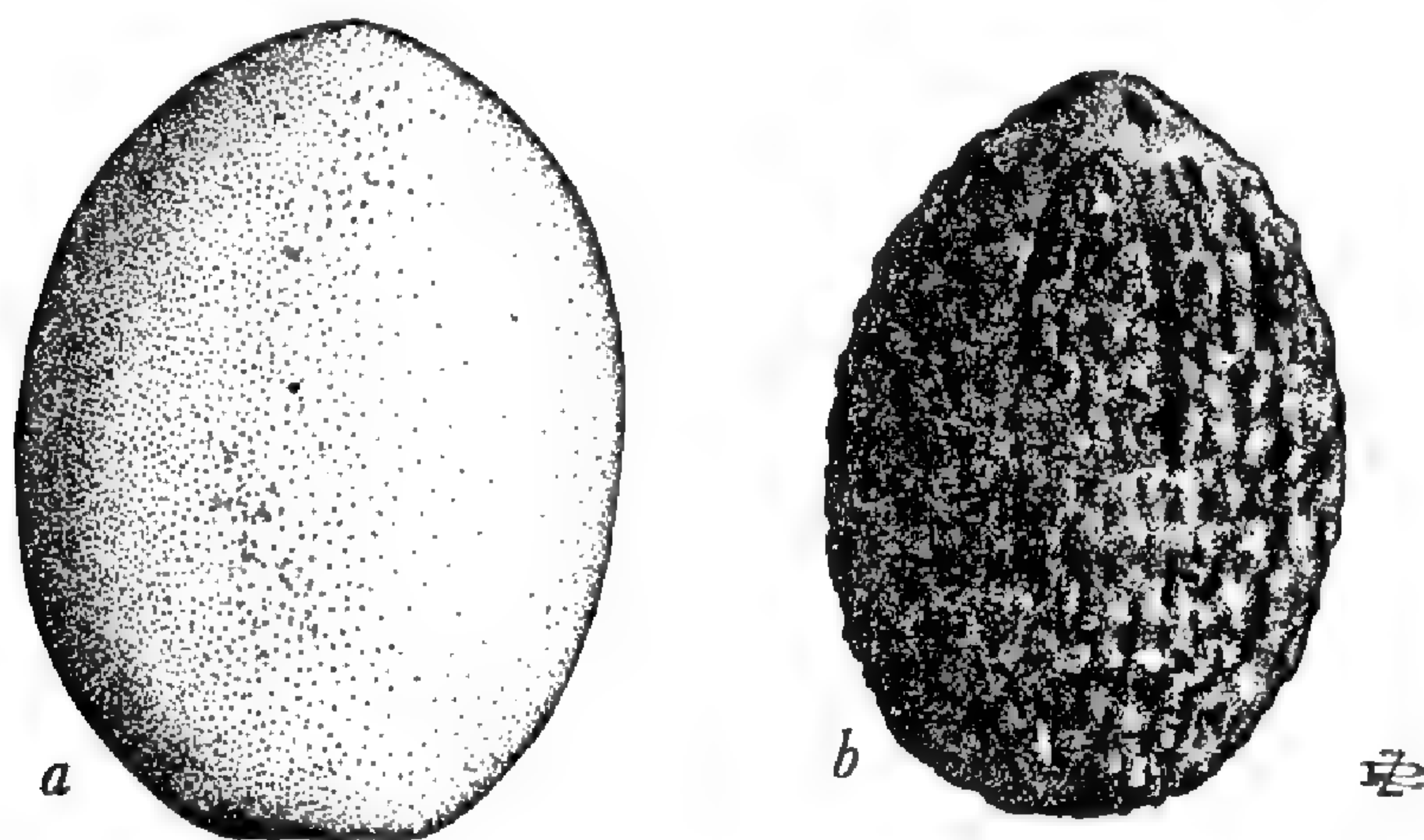


FIGURE 12.—*Vantanea macrocarpa*, $\times 1$ (*Ducke* 2230): *a*, fruit; *b*, endocarp

lustrous above, costa flat, secondary nerves slightly visible, lesser veins obsolete; with thick midrib beneath, secondary nerves slender but prominent, 16–18 on each side, subspreading arcuately connected near the margin; minor veins few and obscure; some minute glands more or less seriate, conspicuous.

Inflorescence cymose-paniculate, axillary and terminal, much shorter than the leaves; the peduncle short, stout; the branchlets thick, articulate, angled, minutely hirtellous. Pedicels thick, short, about 0.5 mm. long, hirtellous. Bracts and bracteoles deciduous, thickish, embracing, ovate, obtusiuscule, 2.5–1.5 mm. long, tomentulose outside. Calyx cupular, about 1.5 mm. high, thick, pubescent-hirtellous, lobate, the lobes subrotundate. Petals white, linear, subacute, glabrous, about 1 cm. long, 1.5–1.8 mm. wide. Stamens about 70, the filaments slender, minutely papillose-verruculose, flexuous, unequal, 6–8 mm. long, at base united in a 2 mm. long tube. Anthers oblong, about 0.9 mm. long, with 8 basal, ellipsoid lobes, the connective fleshy, elongate, subacute. Disk cylindric 1.8 mm. high, glabrous, with dentate-fimbriate margin. Ovary glabrous, 1.5 mm. high, 5-loculate, cells biovulate. Style erect, glabrous, 7–8 mm. long. Stigma obtuse. Drupe ellipsoid, rounded at both ends or obtuse at apex, almost smooth, 4.6–10 cm. long, 3.6–4.5 cm. broad. Exocarp coriaceous when dry, about 3 cm. thick. Endocarp ellipsoid-ovoid, rounded at base, obtuse at apex; the specimen seen 4 cm. long by 3 cm. broad, deeply and anfractuosely alveolate-rugose, the rugosities connected with about 10 large, irregular cavities. The opercula broadly oblong, about 3.4 cm. long and 9 mm. broad, inconspicuous because corrugations entangle their margins. Only one seed and one fertile cavity in the specimen seen, oblong, 2.6 cm. long, 4 mm. thick.

Vantanea macrocarpa, usually a large rain forest tree with white flowers, is known only from the uplands of the Manaos region in Brazil. “Uchy rana” is its common name.

BRAZIL: AMAZONAS: Manaos, silva terris altis ultra flores, arbor magna floribus albis odoratis, 9–III–1937, *Ducke* 30133 (P, S, U, US); *Ducke* 416 (A, NY, S, US). Manaos, prope cataractas flum.; taruma silva non inundabili; arbor magna floribus albis, 25–IV–1932, *Ducke* 20427 (US, P, S, US, RB, isotypes); *Ducke* 21357 (Y); photos F.M. 35174 at Paris. Rio Taruma, mata da terra firme perto da cachoeira alta; arvore grande, flor branca perfumada, 22–II–1949, *Ducke* 2230 (IAN, MG).

12. *Vantanea tuberculata* Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 4:30. 1938. FIGURES 13; 14,c

Type: *Ducke* 30134, Brazil, Amazonas.

Large tree; branchlets brownish, lustrous, glabrous. Leaves coriaceous, brownish when dry, glabrous. Petioles thick, 3–4 mm. long. Blades entire, obovate-elliptic, cuneate at base, obtuse or rotundate

at the apex, 8–11 cm. long, 4.5–6 cm. broad; rather smooth above, costa slightly distinct, smaller nerves almost obsolete; beneath with prominent midrib, the secondary nerves about 10 on both sides, slightly prominulous or almost inconspicuous, near margin arched-connected, minor veins obsolete. Drupe ellipsoid, rounded at both ends, 6.6–8 cm. long, 4.6–6 cm. broad. Exocarp very thick, strongly tuberculate, coriaceous when dry, 8–10 mm. thick. Endocarp heavy, hard, woody, about 5 cm. long, 3.5 cm. broad (in the specimen seen),

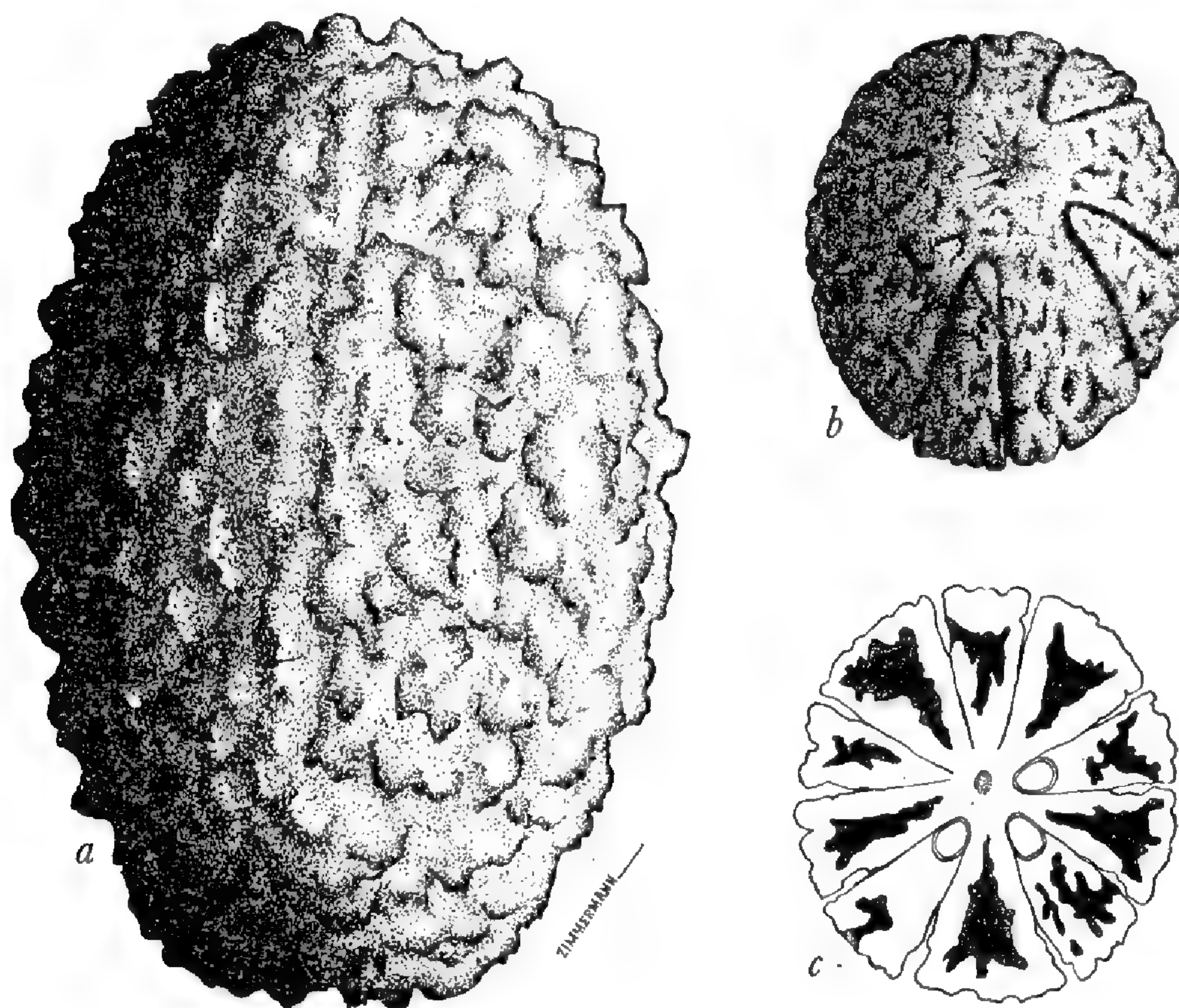


FIGURE 13.—*Vantanea tuberculata*, $\times 1$ (Ducke 30134): *a*, fruit; *b*, endocarp, apical view; *c*, transection.

strongly and deeply anfractuose-rugose, inside with 10 irregular empty cavities (5 in the valves, 5 larger alternating). The 5 opercula (or valves) longitudinal, oblong, subacute at apex. Often only 1 to 3 seeds well developed, oblong, protected by the opercula.

V. tuberculata is known only from its type locality in Amazonas, Brazil. The flowers of the species are unknown, but the structure of the fruit leaves no doubt as to its inclusion in *Vantanea*. The endocarp is like that of *V. macrocarpa*, but the thick warty pericarp distinguishes *V. tuberculata* from all other species of *Vantanea*.

BRAZIL: AMAZONAS: São Paulo de Olivença, Rio Solimões, silva non inundabili, arbor magna, 6-II-1937, Ducke 30134 (isotypes, US, U).

13. *Vantanea guianensis* Aubl. Pl. Guian. 1:572. 1775.—Benth. in Hook. Journ. Bot. Kew Misc. 5:98. 1853.—Urb. in Mart. Fl. Bras. 12(2):452. 1877.—Ducke, Arch. Jard. Bot. Rio Janeiro 3:179. 1922; 5:143, pl. 17, figs. 42a, 42b. 1930.—Arch. Inst. Biol. Veget. Rio Janeiro 4:30, 31. 1937.

FIGURES 14,a-b; 15; PLATE 3

Lemniscia guianensis Gmel. Syst. Nat. 817. 1791.

Lemniscia guianensis Raeuschel Nomencl. Bot. ed. 3; 156. 1797.

Lemniscia floribunda Willd. Sp. Pl. 2:1172. 1800.

Lemniscia floribunda Sprengel, Syst. 2:600. 1825.

Type: *Aublet*, French Guiane, Comté de Gêne.

Large trees with brownish-green, glabrous, subterete lenticellate branchlets. Leaves coriaceous, flexible, glabrous. Petioles 6–12 mm. long, flat and sulcate above. Blades entire, elliptic or oblong-elliptic, obtuse-cuneate at base and decurrent on the petiole, attenuate, shortly and obtusely acuminate at apex, 6–14 cm. long, 2.7–6 cm. broad; more or less lustrous above with prominent and thin costa, secondary nerves slightly prominulous, lesser veins few and almost inconspicuous; beneath with a thick midrib, 13–15 pairs of prominulous, slightly ascendent arcuate-anastomosate secondary nerves, the minor veins reticulate, less conspicuous.

Inflorescences axillary and terminal, shorter than the leaves, cymose-paniculate, subcorymbiform, rich in flowers, the peduncle stout, short, subterete, glabrous, the branchlets angled, glabrous.



FIGURE 14.—a, *Vantanea guianensis*, $\times \frac{1}{3}$ (Ducke 200); b, *Vantanea guianensis*, bud, $\times 1\frac{1}{3}$; c, *Vantanea tuberculata*, leaf, $\times \frac{1}{2}$ (Ducke 30134); d, *Vantanea parviflora*, $\times \frac{1}{3}$ (Ducke 23425).

Bracts soon deciduous, embracing, ovate, about 1 mm. long. Pedicels rather thick, smooth, glabrous, 2–5 mm. long. Calyx thick, deep-cupular about 4 mm. long, glabrous, slightly dentate with obtuse teeth, glandular outside. Petals red or purple, linear, acutish, glabrous, about 3 cm. (up to 4 cm.) long, 2.5 mm. broad. Stamens 64–80, glabrous, filaments flexuous, 25–32 mm. long, united at base in 5–7 mm. long tube. Anthers 1 mm. long, oblong-ellipsoid, lobes 4, oblong, 0.8 mm. long, the connective rather thick with a short, acute tip. Disk tubular, thick, glabrous, 1.5 mm. high with almost smooth margin, encircling the ovary. Ovary ovoid, about 2 mm. high,

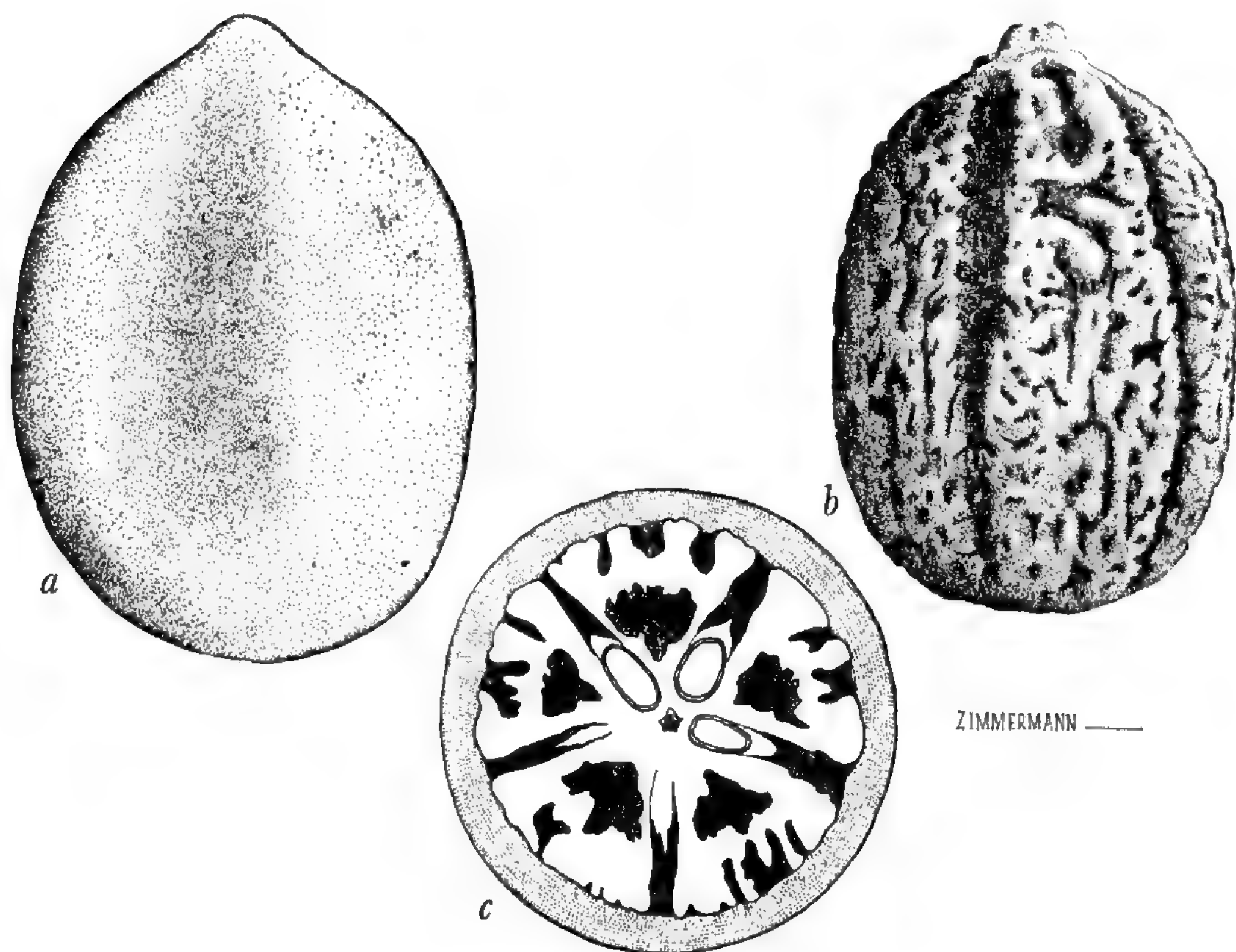


FIGURE 15.—*Vantanea guianensis*, $\times 1$ (Ducke 200): *a*, fruit; *b*, endocarp; *c*, transection.

glabrous, 5-celled, the cells biovulate. Styles flexuous, glabrous, 30 mm. long or longer. Stigma obtuse. Drupe ellipsoid-ovoid, almost smooth, about 6 cm. long, 4.5 cm. broad. Exocarp carnose, 3–5 mm. thick and coriaceous when dry. Endocarp 5×3.8 cm., hard, woody, ovoid-ellipsoid, broadly rounded at the base, abruptly and obtusely apiculate-contracted at the apex, deeply anfractuose-rugose with encephalouslike aspect; five longitudinal, deep and narrow furrows. At the bottom of each furrow a hidden longitudinal, long, narrow operculum (valve). Inside irregular empty cavities alternate with the furrows. The seeds oblong, about 3.2 cm. long and 0.3 cm. thick,

only 2 or 3 developed, at bottom of the grooves, protected by the opercula.

V. guianensis is a medium-size or large tree of humid forests on elevated land, displaying inflorescences of large crimson flowers. Its fruit are of the size of an apricot with a fleshy, insipid, scarcely fatty mesocarp and a hard and corrugated endocarp. According to Schomburgk, these endocarps cut in halves are used as neck ornaments by Guiana Indians. Aublet quoted the native name "Iouantan" as the Caribbean name for the species, on which he based the generic Latin name. Urban (p. 453) gave the Caribbean name the spelling "Schuantan." In Brazil it is known as "uchi-rana" or "achuá-rana."

The species is widely distributed in Venezuela, British and French Guiana, and throughout the middle and lower Amazon Valley.

VENEZUELA: AMAZONAS: Río Casiquiare, Ríos Pacimoni-Yatua, occasional along Río Yatua, 20–25 km. above Piedra Araucana, tree 15–25 m., flowers brilliant pink, 30–IX–1957, *Maguire, Wurdack, & Maguire* 41640 (NY, US).

BRITISH GUIANA: Roraima, 1842–43, *Schomburgk* 982 (BM, NY, P). Corentyn River, *Schomburgk* 1581 (BM, US). "British Guiana" ex Herb. Benthamianum, *Schomburgk* 47 (K).

FRENCH GUIANA: Gourdonville, 2–VIII–1914, *Benoist* 1530 (P). Without locality *Melinon* 100 (US). "Habitat in America meridionali, specimen e collect: Aublet: misit Gener: Barron: Dans Banks, a: 1782"; this *Aublet* specimen may be considered as the holotype (S).

BRAZIL: AMAZONAS: Manaus, Estrada do Aleixo, silva non inundabili; arbor magna floribus roseo purpureis, 20–V–1936, "uchi-rana," *Ducke* 200 (IAN, NY, S, US, A). Manaus, silva non inundabili, arbor mediocris, floribus laete purpureis, 31–III–1932, *Ducke* 23814 (U, S, US). Manaus, beira do Rio Tarumã, t.f. baixa; arvore 10 m., flores vermelhas, vistosas, sem odor, 7–VIII–1949, *Frões* 24936 (IAN). PARÁ: Belém, cultivada no IAN; arvore grande, flor muito vistosa, roseo avermelhada, 25–VIII–1953, *Pires* 4518 (IAN, NY, U, US). Santa Isabel ad viam ferream Belém-Bragança, silva humosa; arbor magna floribus coccineis, 10–IX–1922, *Ducke* 17783 (U). Peixeboi (Belém-Bragança), matta, 21–X–1907, "uchi-rana," *Siqueira* 8775 (MG, BM, US, P). Caraparú (Belém-Bragança), matta, 6–IX–1908, *Museu Goeldi* 9664 (MG, BM, P, US). Utinga, Belém, 13–VIII–1914, *Ducke* 15451 (MG). Utinga, 13–VIII–1914, *Ducke* 15415 (MG). Belém, Estrada Providencia, Tapaná, matta da terra firme, arvore grande, flor carmesin, 31–X–1944, "uchi-rana," *Ducke* 1647 (IAN). Breves, transecto para inventario forestal 101–1, 7–30–VII–1956, *Pires, Frões, & Silva* 5380 (IAN). Pará, sine loco, *Jobert* 362 (P). Rocky riverside below Fiafun Mount by falls Mapueva River, headwaters Acarai Mountains; 8 in. × 45 ft. leaning tree with rough bark; orange brown ½ in. slash yellow splintery wood; leaves alternate, ovate, lanceolate, glossy, leathery; recurved terminal inflorescences of bright rose pink flowers with linear petals to 1 in. recurved, caducous and stamens of same colour to 1½ in.; flower shoots erect; leaves hanging; fruit (young) green, ovoid, with terminal point to which persistent stigma attached, after rested in by ants, *Forest Dept.* G. 600 (NY). Distrito Acará Thomé Assu up Rio Acará, 5 km. river bank in virgin forest, alt. 35 m., tree 18 m. high, bright cerise flower standing above crown, very ornamental, 5–VIII–1931, *Mexia* 6049 (A, BM, GH, NY, U, S, US). RIO DE JANEIRO: Restinga de Cabo Frio, 29–XII–1877, *Glaziov* 10078 (P).

14. *Vantanea parviflora* Lam. Journ. Hist. Nat. par. 1:145, pl. 7. 1792.—Urb. in Mart. Fl. Bras. 12(2):454. 1877. FIGURES 5,a-e; 7,c-d; 14,d
Vantanea cupularis Huber, Bol. Mus. Goeldi 6:83. 1910.—Ducke, Arch. Jard. Bot. Rio Janeiro 3:179. 1922.—Arch. Inst. Biol. Veget. Rio Janeiro 4:29. 1937.

Type: *Le Blond*, French Guiana.

Large tree with subterete, lenticellate, glabrous, rarely puberulous branchlets. Leaves coriaceous, flexible, glabrous or sometimes appressed-pilose, or midrib hirtellous beneath. Petiole semiterete, sulcate above 5–15 cm. long. Leaf blades entire, elliptic, more or less elongate, obtusely cuneate or cuneate at base, obtuse, emarginate, obtuse-acuminate or even subrotundate at apex, 5–10 cm. long, 2–5.5 cm. broad; greenish-brown or olivaceous above with distinct flat midrib and prominulous secondary and smaller nerves; beneath more or less lustrous, cuperous-brownish with prominent midrib, 9–10 slender but prominent ascendent secondary nerves on each side, arcuate and united near the margin, smaller veins reticulate, prominulous.

Panicle cymose-dichotomous, corymbiform, axillary or terminal, shorter than the upper leaves; the axis and branchlets more or less compressed, pubescent-hirtulous. Bracts ovate, subobtuse, minutely pubescent, soon deciduous, 1 mm. long. Pedicels about 1–2 mm. long, moderately thick, minutely pubescent-hirtulous. Calyx broadly cupular scarcely 1 mm. long, 2.5 mm. diameter, puberulous outside, the margin ciliolate, entire or slightly undulated. Petals white, linear, rather thick, 7–8 mm. long, pubescent outside, hairs abundant, retrorse, subappressed, glabrous inside, estivation contorted. Stamens 80–120, filaments glabrous, 2–3 seriate, united at base, unequal, 5–7 mm. long. Anthers about 0.8–1 mm. long, dorsifixed with 4 elliptic-oblong lobes, the connective with a long, thickish, acute tip. Disk annular, thick, densely hirt-tomentous, 1–1.5 mm. high, girdling the ovary. Style columnar, about 3.5 mm. long, subglabrous, only some long, spreading hairs near its base. Ovary 2.5 mm. high, ellipsoid, villosio-hispid with long hairs, with 5 biovulate cells. Stigma obtuse, glutinous. Drupe ellipsoid, 2.5–2.8 cm. long, 2.2–2.5 cm. broad, becoming glabrous; the endocarp woody like a nut, rugose, 2.1–2.5 cm. long, 1.8–2 cm. broad, with 5 longitudinal broad ribs and valves.

One specimen from French Guiana, *Wachenheim* 179 (P), has globose drupes and endocarp. The drupe is about 24 mm. in diameter, with a 1–2 mm. thick ectocarp. The endocarp is densely ligneous, rugose, with 12 sulci, and 6 longitudinal valves. The specimen seen has only two seminal cavities. This specimen and another closely related one from French Guiana do not show any other difference from the Brazilian specimens, for which reason they are considered conspecific.

The typical *V. parviflora* is completely glabrous except for the inflorescence. Only a few specimens from Brazil show appressed, sparse hairs on the underside of the leaf or a slightly hirtellous pubescence on the midrib and petiole; these forms are transitional toward the variety *puberulifolia*.

This large or medium-size tree is much spread out in the uninundatable rain forests of French Guiana, the Brazilian States of Para and Amazonas, and the Venezuelan State of Amazonas.

14a. *Vantanea parviflora* var. *parviflora*

VENEZUELA: AMAZONAS: Río Negro, San Carlos and vicinity, tree, flowers white, 9-XII-1947, *Schultes & López* 9267 (COL, IAN, US).

FRENCH GUIANA: "Herb. de la Guyane française, année 1863, boise göelette rouge," *Melinon* 100 (BM, P). "Guyane française," *Melinon* s.n. (US, several specimens in P). Arbor 30-40 pedalis in sylvis Guyannae, ex. herb. *Claude Richard* s.n. (P). Guyane ex Herb. Maire, Herb. Cosson (P). Cayenne, photo F.M. 12592, without collector (from Berlin-Dahlem). Guyane fr. 18-XI-1921, *Godebert Wachenheim* 179, (P); 23-VI-1921, *G. Wachenheim* 489 (P). Route de Saint Laurend a Cayenne km. 13; terrain sain sablonneux inonde à la raison des pluies, fleurs blanches, 6-VIII-1953, "koko" (Paramaka), "gris-gris-bois gaulette," *BAFOG* 48M (P). Route de Charvein à l'Acarouany km. 3 côte sud et à 20 m. de la route "terrain sain." Fruits verts ovoïdes forme et grosseur d'une petite olive, recouverts d'une pubescence blanchâtre par petites grappes à la pointe des rameaux, "boliquin" (Pamaka), "gris-gris rouge," *BAFOG* 102M (P). Route Charvain-Acarouany km. 1; plateau argileux, 10 m. audessus du niveau de l'eau; fleurs non épanouies petites, boutons rosâtres, ovales, 1-2 mm., en bouquet à l'extrémité des rameaux, "adougoue" (Paramaka), 24-IX-1954, *BAFOG* 220M (U). Côte gauche et à 10 m., plateau peu élevé, environ 5 m., sabro-argileux assez profond, fleurs blanchâtres en grappes á l'extrémité des rameaux, étamines nombreuses, *BAFOG* 247-M (U).

BRAZIL: AMAZONAS: Manaus, Estrada do Aleixo, silva non inundabili, arbor sat magna floribus albis odore forti, mata da terra firme, 3-IV-1936, 31-VII-42, *Ducke* 157 (A, IAN, MG, NY, S, US). Manaus, silva non inundabili versus flores; arbor media floribus albis odore forte, 8-VIII-1929, *Ducke* 23426 (P, S, U, US). Manaus, Igarapé da Cachoeira Baixa do Tarumá, terra arenosa, capoeira; arvore 15 m., flor branca, 21-IX-1955, *INPA* 1809 (MG 21541). Rio Urubú, igarapé Sangana; terra firme, alta, floresta central, arvore 18 m. X 35 cm., 2-X-1949, *Frões* 25459 (IAN). Rio Urubú, São José das Pedras, terra firme, alta, floresta alta; arvore de 18 m. X 35 cm., flores brancas, 11-IX-1949, *Froes* 25185 (IAN). Basin Rio Juruá, near mouth of Rio Embira (tributary of Rio Tarauaca) tree 110 ft. high, on terra firma, 21-VI-1933, *Krukoff* 4956 (A, BM, M, NY, S, U, US). Rio Solimões, São Paulo de Olivença, arbor sat magna floribus albis odore fortissimo, 19-VIII-1929, *Ducke* 23429 (P, S, U, US). Basin Rio Madeira, Municipality Humaytá, on plateau between Rio Livramento and Rio Ipixuna, tree 20 ft. on campinarana alta, *Krukoff* 7120 (IAN, NY, S, US, U). PARÁ: Santa Rosa (Belém-Bragança), matta, "uchi-rana," 10-X-1908, *Museu Goeldi* 9723 (MG, BM, P, US). Moêma ad viam ferream Belém-Bragança, 30-VIII-1908, *Huber* 9583 (S, U, isotype of *Vantanea cupularis* Huber); photo F.M. 12588 at Berlin-Dahlem. Moêma, matta, 17-IX-1908, *Museu Goeldi* 9670; 30-VIII-1908, *Museu Goeldi* (Huber) 9583 (P, US). Utinga (Belém-Bragança), silva non inundabili; arbor magna, floribus albis, matta da terra firme, 27-VIII-1941, *Ducke* 781 (IAN, MG, US). Santa Isabel, Belém-Bragança,

27-IX-1908, *Museu Goeldi* 9680 (B, US, MG). Utinga-Providencia, 28-VIII-1914, *Ducke* 15467 (MG). Belém, Horto Mocambo (Reserva Florestal), arvore, VIII-1951, *Pires* s.n. (US). Perto do Igarapé Arapijó municipio de Breves, 2-I-1955, 7-30-VII-1956, *Pires, Fróes, & Silva* 5105, 4954 (IAN). Obidos, silvis non inundatis, inter lacuna Mamaurú et Castanhal do Prior; arbor media floribus albis odoratis, 14-IX-1926, *Ducke* 20426 (U, S, US). Juruty Velho, silva non inundabili, arbor sat magna, 24-XII-1926, *Ducke* 20428 (US). Trombetas, entre Cuminámirim e Ariramba, 12-X-1913, *Ducke* 14962 (MG, BM, P, US). Region Boa Vista, hab. terra firme, "uxy bravo," 10-X-1932, *Capucho* 483 (IAN). Without locality, *Herb. John Miers* 6167 (BM).

14b. *Vantanea parviflora* var. *puberulifolia* Cuatr. var. nov.

Cum typo differt: Folia subtus sparse adpresse pilosula. Petiolus costaque subtus breviter hirtula. Ramuli terminales hirtu-puberuli.

Type in the U.S. National Herbarium, No. 1518624, collected in a nonflooded forest at Fonteboa (Solimões River), State of Amazonas, Brazil, September 6, 1929, by A. Ducke, No. 23428. Isotypes in Museum National d'Histoire Naturelle, Phanerogamie, Paris, and in Naturhistoriska Museum, Stockholm.

This variety is characterized by its appressed puberulous leaves beneath and short-hirtellous midrib, petioles, and young branchlets. The typical form of the species has completely glabrous leaves and branchlets. Only a few specimens from Brazil are very shortly and scarcely puberulous on the underside of the leaves or have the midrib puberulous (*Ducke* 23429, 20428, *Schultes & López* 9267, *Krukoff* 4956, 7120, *Museu Goeldi* 9723); they are intermediate forms of this variety. *Ducke* 23428 has the apical appendix of the anthers more slender and longer (up to twice as long as the thecae), but this condition is not characteristic of the variety because examination of many specimens shows a great variability.

BRAZIL: AMAZONAS: Rio Solimões, Fonteboa, *Ducke* 23428 (type). Manaus, silva non inundabili; arbor magna floribus albis odore fortissimo, 10-III-1929, *Ducke* 23427 (US). Manaus, prope Cachoeira Grande, silva non inundabili; arbor sat magna, floribus albis, odore fortissimo, 8-VIII-1929, *Ducke* 23425 (US, S, U).

Tribe Humirioideae

Humirioideae Cuatr., tribus nova Humiriacearum.

Stamina definita (10-30) antheris 2-4 thecis unilocularibus disjunctis, basim abscisso-dehiscentibus. Genus typicum *Humiria* (Aubl.) St. Hilaire.

2. *Duckesia*

Duckesia Cuatr., gen. nov.

Sepala suborbiculata basi coalita imbricata. Petala 5 libera oblonga praefloratione contorta vel cochleari. Stamina 20-25 filamentis subulatis paulo compressis papillosis inaequalibus basi in

tubum brevem coalitis. Antherae lineari-lanceolatae dorsifixae, thecis 4 unilocularibus disjunctis globosis vel globoso-ellipsoideis duobus basilaribus duobus subparte media utroque latere instructis connectivo acuto, tantum 5 oppositipetalae fertiles. Discus squamis 10 liberis subulatis crassiusculis. Ovarium ovoideum 5-loculare loculis episepalis uniovulatis, ovulis anatropis raphe ventrali. Stylus stamina attingens stigma anguste capitato breviter 5-lobato. Drupa ovoidea sublaevis exocarpio crasso. Endocarpium spongioso-lignosum resinoso-lacunosum verrucosum subapicem 5-foraminatum lateraliter longitudinaliterque 5-valvatum. Semina oblonga. Arbores foliis simplicibus persistentibus coriaceis vel subcoriaceis petiolatis. Inflorescentiae axillares breves cymoso-paniculatae plus minusve dichotomae. Typus: *Sacoglottis verrucosa* Ducke.

Sepals 5, suborbicular, imbricate, united in a cup. Petals 5, free, linear-oblong, thick-membranaceous, the estivation contorted or cochlear. Stamens 20–25, biseriate, glabrous, the filaments united at base, complanate, subulate, papillose, alternating in three dimensions. Occasionally some shorter staminodia present. Anthers linear-lanceolate, glabrous, dorsifixed, usually only 5 fertile; the connective lanceolate, carnose; the thecae 4, unilocular, dissociated, subglobose or ellipsoid, 2 attached at the base, the other 2 laterally at the middle, dehiscing by accidental pulling away. Disk formed by 10 subulate free scales surrounding the ovary. Ovary glabrous, 5-locular, each cell with a single anatropous, pendulous ovule. The carpels opposite the sepals. Style erect, as high as the stamens. Stigmas forming a 5-lobate head. Drupe large, ovoid, almost smooth, with thick exocarp, coriaceous and fragile when dry. Endocarp strongly verrucose, spongy-lignose, resinous-lacunose, five-foraminate at the apex, laterally with 5 longitudinal oblong germinal valves or opercula. Seeds few, oblong. Evergreen trees with alternate, thin-coriaceous, petiolate, serrate leaves; the teeth ending with an erect deciduous gland. Inflorescences axillary, small, cymose-paniculate, furcate below, upwards alternate branching. Bracts persistent.

Duckesia differs from *Sacoglottis* in the structure of the anthers with a long connective and four unilocular thecae, two of them being at the base, the other two being higher up and lateral, and in the valvate endocarp. The endocarp is strongly rugose-tuberculate, somewhat corky-woody, and provided with five longitudinal opercula as is typical in *Vantanea*. From *Vantanea* it differs in the four unilocular thecae of the anthers, the number of stamens, and the spongy structure of the endocarp full of small resinous cavities. The fertile stamens, which are opposite the petals, originate from an inner whorl, which is concrescent with the outer whorl. (See figs. 3, 16, 19.)

This genus is named in honor of Adolpho Ducke, the discoverer

of the plant and the most outstanding Amazonian botanist and plant-explorer of this century.

Duckesia has only one species, which is limited to Amazonian Brazil.

1. *Duckesia verrucosa* (Ducke) Cuatr., comb. nov.

Sacoglottis verrucosa Ducke, Arch. Jard. Bot. Rio Janeiro 3:177, pl. 10b. 1922; 5:142, pl. 14 figs. 35a, 35b. 1930.—Arch. Inst. Biol. Veget. Rio Janeiro 4:26. 1937.

FIGURES 16,g-k; 18,b; 19,d-e

Type: *Ducke* 10815, Brazil, Pará, Obidos.

Tree with thin, minutely hirtellous-pubescent terminal branchlets. Leaves small, thin-coriaceous, sessile or subsessile. Petiole 0–1.5 mm. long, rather thick, pubescent. Blade lanceolate, cuneate, sessile or narrowed to a very short petiole at base, acuminate or cuspidate at apex, serrate-crenulate at margin, 3–8 cm. long, 1–2.3 cm. broad; above smooth, glabrous or when young with minute hairs on the conspicuous midrib, the other nerves obsolete; the midrib

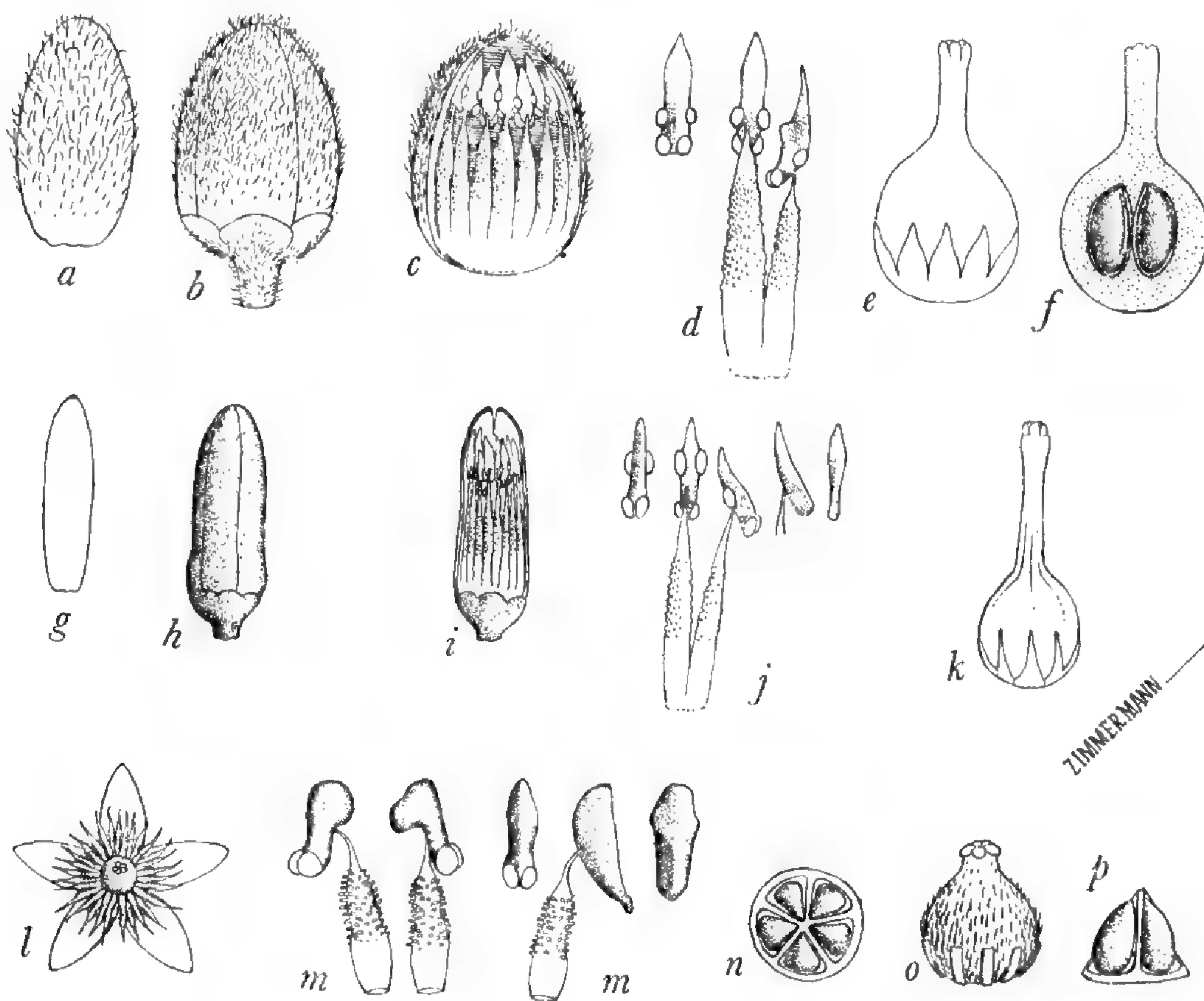


FIGURE 16.—a-f, *Endopleura uchi* (Baker 58): a, petal; b, bud; c, bud with 2 front petals removed, $\times 5$; d, detail of stamens, $\times 10$; e, gynoecium and disk, $\times 10$; f, longitudinal section of ovary $\times 10$. g-k, *Duckesia verrucosa* (Ducke 16325): g, petal, h, bud; i, bud with frontal petals removed, $\times 5$; j, details of stamens and anthers with 2 sterile anthers right, $\times 10$; k, gynoecium and disk, $\times 10$. l-p, *Hylocarpa heterocarpa* (Pires 708): l, open old flower (with fallen anthers), $\times 5$; m, stamens $\times 10$, 2 sterile anthers at right; n, transection of ovary, $\times 10$; o, gynoecium and disk, $\times 10$; p, position of ovules in the ovary, $\times 5$.

beneath prominent and minutely pubescent or puberulous, elsewhere glabrous or scarcely pilose, the 12–14 pairs of secondary nerves slightly prominulous, ascending, near the margin arcuate-anastomosing, the minor nerves almost obsolete; when young the teeth end with a linear erect deciduous gland 0.4 mm. long.

Inflorescence axillary, much shorter than the leaves, cymose-paniculate, divaricate, the branchlets thin, usually alternate, furcate below. Peduncles and branchlets minutely hirtellous-pubescent. Bracts ovate-lanceolate, amplexant, 1–0.5 mm. long, puberulous. Pedicels thick, 0.4–0.5 mm. long, articulate with short peduncles or sessile. Sepals suborbicular, about 0.6 mm. long, minutely ciliate at margin. Petals linear-oblong, subacute, glabrous, about 3.5 mm. long, 1 mm. broad. Stamens 20–25, glabrous, the filaments 1.7–2.2 mm. long, complanate, subulate, acute, minutely papillose, united at base; the 5 opposite the petals larger. Anthers linear-lanceolate, glabrous, 1 mm. long, dorsifixed, only 4–5 of them (those of the larger filaments) fertile; of 4 thecae 2 short-ellipsoid, basal, the other two oblong-ellipsoid, lateral on the middle; the connective lanceolate, subtriquetrous, carnose; the other 15–20 anthers sterile. Some shorter additional staminodial filaments may also be present. Style columnar, glabrous, about 1.5 mm. long. Stigma subcapitate-pyramidal, slightly 5-lobate. Scales of disk 10, subulate, rather thick, 0.5 mm. long, free. Ovary ovoid, glabrous, about 1 mm. high, furrowed, 5-locular, the cells uniovulate, the ovules ellipsoid-oblong, 0.6 mm. long. Drupe short-ovoid or subglobose, about 7 cm. long and 6 cm. in diameter, almost smooth; exocarp 10–13 mm. thick. Endocarp (*Ducke* 16764 in US) ovoid, abruptly acute at apex, 3.5 cm. in diameter, spongy-lignose, densely resinous-lacunose, acutely verrucose, 5-foraminate below the apex, conspicuously 5-valvate lengthwise. The seeds oblong, 2 seen in the specimen.

Duckesia verrucosa is a large tree of the rain forest of firm land in the middle Amazonian region. It has been discovered and collected only by Adolfo Ducke, who writes about it thus: "This species produces the fruit 'uchy-curua' or 'uchy-coroa' ('uchy' meaning warty, referring to the protuberances of its stone), which can be found on the markets of Manaus and Obidos where it is eaten raw. Wood brown-gray purplish, rather hard and dense, with no known uses."

BRAZIL: AMAZONAS: Manaus, Estrada do Aleixo, mata das terras altas argilosas; arvore muito grande, flor verde con estames amarelos, fruto comestivel, "uchi curúa," 23–VIII–1947, *Ducke* 2108 (IAN, MG, US, PU). Tapajoz medio, Cachoeira do Mangabal, "uchi-curúa," 13–II–1917, *Ducke* 16764 (MG, US). PARÁ: Obidos, matta da terra firme, "uchy-curúa," 18–X–1913, *Ducke* 14992 (MG). Obidos, silva non inundabili, arbor magna floribus viridibus odoratis, "uchy-curúa," 11–VIII–1916, *Ducke* 10815 (isotypes, NY, S, U). Same data,

Ducke 16325 (MG number; holotype, MG; isotypes, PS), photo F.M. 12603 from Berlin. Territorio do Guaporé, VIII-1952, *Silva* 416 (IAN).

3. *Endopleura*

Endopleura Cuatr., gen. nov.

Sepala 5 orbicularia imbricata basi coalita. Petala 5 libera oblonga praeefloratione contorta vel cochleari. Stamina 20-30 filamentis crassiusculis leviter angulatis papillosis biseriatis inaequalibus 5 longioribus oppositisepalis inferiore parte coalitis. Antherae connectivo crassiusculo elongato acuto, thecis 4 disjunctis subglobosis 2 ad basim utroque latere 2 lateralibus supra basim, interdum 2 vel omnibus thecis sterilibus. Discus 10 squamis anguste ovato-triangularibus basi coalitis. Ovarium subglobosum 5-loculare loculis episepalis uniovulatis ovulis anatropis raphe ventrali. Stylus brevis. Stigma capitatum 5-lobatum. Drupa ellipsoidea exocarpio fibroso-farinaceo; endocarpio lignoso eminente 5-alato-costato costis basi excepto bifidis cum sectione figura 10-radiata, 5-valvato; mesocarpio inter costas dense fibroso. Semina oblonga 5 vel saepe tantum 1-3 evoluta. Arbores foliis simplicibus alternis persistentibus coriaceis vel subcoriaceis petiolatis. Inflorescentiae axillares cymoso-paniculatae bracteatae bracteolataeque. Typus: *Sacoglottis uchi* Huber.

Sepals 5 suborbicular, imbricate, united at base. Petals 5, free, oblong, thick, the estivation contorted or cochlear. Stamens 20-30 biseriate, glabrous; the filaments thick, angulate, papillose, united at base, alternating in different dimensions, the largest opposite the sepals. Anthers dorsifixed with thick, elongate, acute connective, the thecae 4, unilocular, dissociated, subglobose, 2 attached at base, other two lateral above the base, sometimes 2 thecae or rarely all 4 sterile; irregular dehiscence when pulling away the sacs. Disk formed by 10 ovate-triangular, thick scales, united at base. Ovary glabrous, suborbicular, 5-locular, cells uniovulate, ovules anatropous, pendant with ventral raphe. Carpels opposite sepals. Style short. Stigmas lobate-capitate. Drupe large, ellipsoid, with exocarp fibrous-farinaceous, coriaceous when dry. Endocarp woody, with 5 apical foveola, with 5 ribs strongly elevated and divided into 2 except at the end, forming 10 strong, woody wings which make in section a 10-ray stellate figure; the mesocarp fills the space between the ribs with a compact fibrous structure; inconspicuous linear, germinal valves between the branching ribs at bottom of the furrow. Seeds oblong, rarely all 5 developed, usually only 1-3 becoming ripe. Evergreen trees with alternate, coriaceous, serrate, petiolate leaves. Inflorescences axillary, cymose-paniculate, with trichotomous or dichotomous branching. Bracts persistent. (See figs. 3 and 16-18.)

Endopleura differs from *Sacoglottis* in the four unilocular thecae of the anthers, of which two are basal and the other two located above and laterally, and in the deeply sulcate endocarp, which has five eminent longitudinal bifid winged ribs. The transversal section of *Endopleura* looks like a 10-ray star. Furthermore, the endocarp has narrow, shorter, inconspicuous valves and lacks resinous cavities. *Endopleura* differs from *Vantanea* in the structure of the anthers, the number of stamens, and the shape of the endocarp.

The name “*Endopleura*” is derived from the Greek “endon” (inside) and “pleuron” (rib), the latter referring to the strong ribs of the endocarp.

This genus has only one species, which is endemic to the Amazon basin from Manaus to Belém.

1. ***Endopleura uchi*** (Huber) Cuatr., comb. nov. FIGURES 16,*a-f*; 17; 18,*a*
Sacoglottis uchi Huber, Bol. Mus. Paraense. 2:489. 1898.—Bol. Mus. Goeldi, Pará 4:395, 1904.—Ducke, Arch. Jard. Bot. Rio Janeiro 3:177 1922; 5:142, pl. 14 figs. 34a, 34b. 1930.—Arch. Inst. Biol. Veget. Rio Janeiro 4:26, 1937.

Type: *Huber* 1260, Brazil, Pará, Belém.

Large tree with glabrous, green, more or less angulate, compressed young branchlets. Leaves coriaceous, firm or flexible. Petiole 1–2.3 cm. long, semiterete, pubescent or glabrous, sulcate above, more or



FIGURE 17.—*Endopleura uchi*, $\times 1$ (Ducke 305): *a*, fruit; *b*, endocarp; *c* transection.

less winged at margin. Blade elliptic-oblong or elliptic-lanceolate, abruptly and obtusely cuneate at base, narrowed-acuminate, often cuspidate at apex, serrate and slightly thickened at margin, 8–20 cm. long, 2.3–8 cm. broad; lustrous above with conspicuous lighter midrib, glabrous or with very minute hairs toward the base, the secondary nerves pale, prominulous, the veins conspicuously prominulous-reticulate; dull, glabrous beneath with thick midrib, the 12–14 pairs of secondary nerves thin, prominent, patulous and curvate-anastomosing, the prominulous veins forming a very conspicuous reticulum.

Inflorescences cymose-paniculate, axillary, much shorter than the leaves; the 1-3 cm. long peduncles and branchlets compressed, hirtellous or puberulous, trifurcate below, dichotomous above. Bracts persistent, ovate, amplexant, about 2 mm. long. Bracteoles ovate, subacute, hirtellous-puberulous, minute, about 0.5 mm. long, persistent. Pedicels rather thick, hirtellous-pubescent, 0.2-0.5 mm. long, articulate with 0-1 mm. long, pubescent peduncles. Sepals about 0.7 mm. long, orbiculate, hirtellous-pubescent, united at base. Petals greenish, rather thick, linear-oblong, subacute or subobtuse,

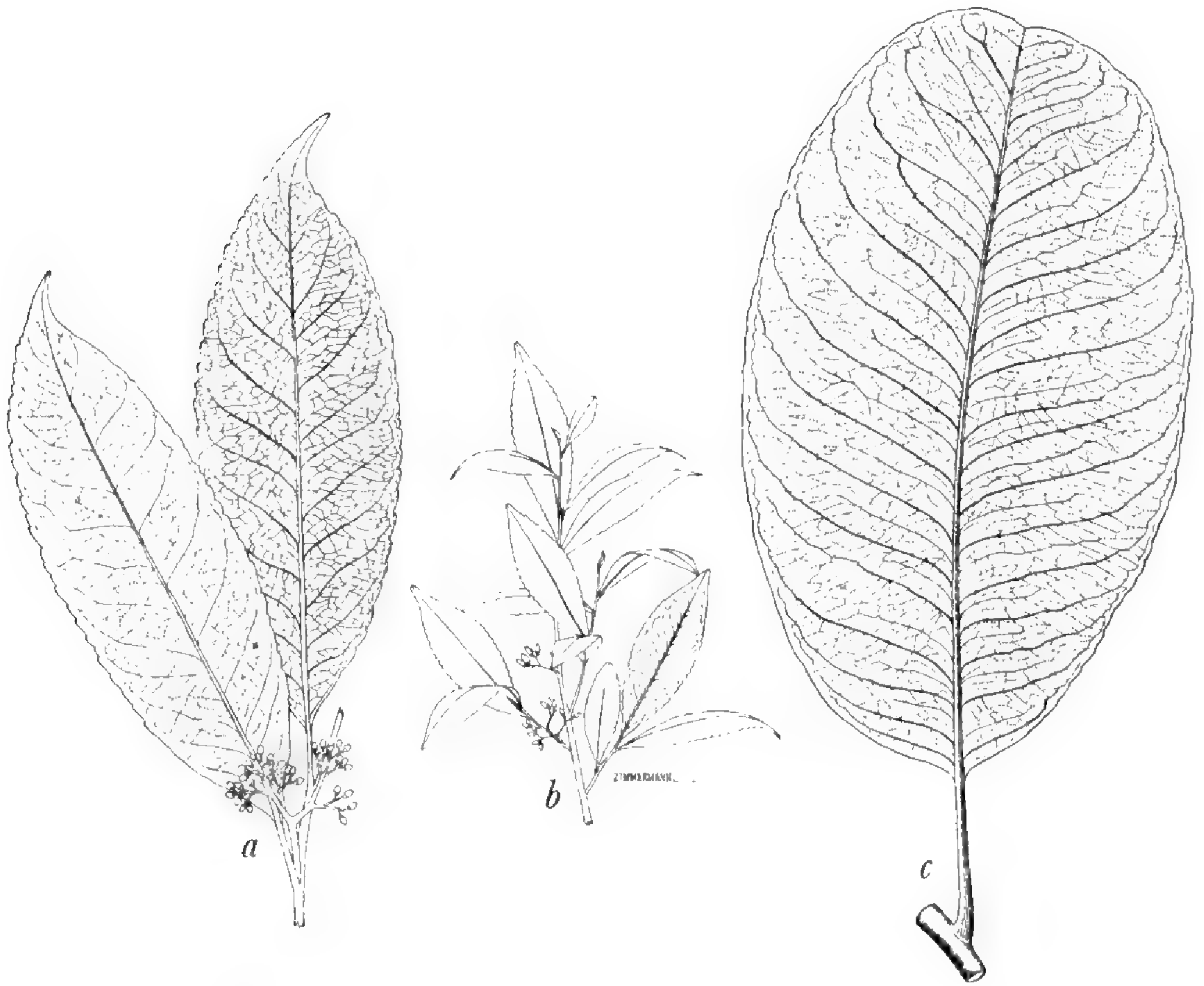


FIGURE 18.—a, *Endopleura uchi* (Ducke s.n., US 1693003), floriferous branchlet, $\times \frac{1}{3}$; b, *Duckesia verrucosa* (Ducke 2108), floriferous branchlets, $\times \frac{1}{2}$; c, *Hylocarpa heterocarpa* (Pires 708), leaf, $\times \frac{1}{3}$.

glabrous inside, hirtellous-pubescent outside, 3-3.5 mm. long, 1-1.4 mm. broad. Stamens 22-30 (mostly 25), the filaments 1.5-2 mm. long, thick, angulate, densely papillose, united in their $\frac{1}{3}$ - $\frac{1}{4}$ lower part, different lengths alternating, the longest with larger anthers opposite the sepals. Anthers about 0.9 mm. long with 4 globose-elliptic, 0.2 mm. long, 2 basal and 2 inferior-sided thecae, the connective lanceolate, acute, about 0.7 mm. long. Sometimes 2 of the thecae of the anthers sterile, rarely all 4. Scales of the disk 10, about 0.6 mm. long, triangular, united at base. Ovary glabrous, subglobose,

0.9–1 mm. high, 5-locular, the cells uniovulate, opposite the sepals. Style stout, longer than the ovary. Stigma capitate 5-lobate. Drupe oblong-ellipsoid, 4–6 cm. long, 2–3.8 cm. in diameter, rounded at both ends; exocarp 1 mm. thick, coriaceous when dry, almost smooth, reddish-brown; mesocarp 2–3 mm. thick, carnose (granulose when dry), resinous. Endocarp woody, deeply 5-grooved, with 5 projecting ribs divided halfway into two, except at one end, giving a 10-radiate shaped section; the tissue between the ribs very compact, fibrous, removable at maturity. Seeds most frequently 2–3, oblong, about 30 mm. long, 7 mm. thick.

Endopleura uchi is widely spread in the Amazon Valley, from Pará to the Purus and Solimões regions. It is a large tree often cultivated at Belém. Ducke writes about it thus: "This species is called 'Uchy' at Belém and is known at the lower Amazonas as 'uchy pucu,' 'uchy' meaning elongated shape. It is found cultivated at the capital and spontaneous in the forests of uninundated lands between Belém and Bragança. The so-called 'uchi-pucú' of the lower Amazon Basin belongs to this species, according to a flowering specimen from the highlands near Cumina-mirim of the Trombetas region. I have also observed this species in the forests of Volta of Xingú, of Gurupá, on the 'serras' between Almeirín and Faro, and in the middle Tapajoz. The fruit found by Huber in the forests of the upper Purus also seem to belong to the species."

BRAZIL: AMAZONAS: Manaus, Pensador, mata da terra firme; arvore grande, flor verde cheirosa, "uchi," "uchi-pucu," 10-VIII-1943, *Ducke* 241 (IAN, MG, S, NY, US, A). Pensador, arvore grande, flor verde, "uchya," "uchy-pucu," 17-VII-1936, *Ducke* 305 (Y, NY). Pensador, silva non inundabilis, arbor magna floribus viridibus odoratis, "uchi," "uchi-pucú," 17-VII-1936, *Ducke* s.n. (US). Manaus, silva non inundabili, arbor magna floribus viridibus odoratis, "uchi," 15-VIII-1931, *Ducke* 23815 (US, S, U). Rio Tonantins, terra firme baixa, arvore de 4 m., flores amareladas, 27-X-1949, *Fróes* 25565 (P, IAN). Region Bôa Vista, habitat terra firme, 8-IX-1932, *Capucho* 430 (IAN). PARÁ: Pará, horto bot. "uchi," 14-VII-1896, *Huber* 239 (MG); photo F.M. 12602. Belém, Jard. Bot., I-VI-1908, *Huber* 940 (M, U). Belém, hort. bot., "uchi," X-1897, *Museu Goeldi* 1260 (Manoel Guedes or Huber) (holotype, MG; isotype, US); *Manoel Guedes* 1260 (US, MG). Bot. Gard. Mus. Goeldi, a fruit-yielding tree long known in Pará as "uchi"; the tree magnificent, becoming very tall with dense rounded top, 1-VII-1908, *Baker* 58 (A, GH, NY, US, U). Belém, Jard. Bot., 1-VI-1908, *Baker* 9401 (MG); *Baker* s.n. (M, S, US). Belém, cultivado, "uchi," X-1897, *Huber* 1260 (isotype, US). Belém, culta et circa urbem spontanea, arbor magna, floribus viridibus odoratis, "uchy," VII-1923, *Ducke* 17779 (US, P, S, U). Belém, arvore 108 ft. não possui cheiro, as flôres novas são enleadas de cipós, madeira a ser estudada pela Universidade de Yale, "uchi," 7-VII-1947, *Black* 47-1001 (Black project 135) (IAN, NY, U, US, VEN, Y). Belém, Inst. Agr. Norte, cafezal antigo, "uchi," folha consistente, 26-IV-1957, *Black* 57-19306 (US). Rio Cuminámirim, Castanhal das Pedras, "uchy-pucú," 13-X-13, *Ducke* 14979 (MG). Rio Xingú, estrada da Volta, "uchi," 20-XII-1916, *Ducke* 16641 (MG).

4. *Hylocarpa*

Hylocarpa Cuatr., gen. nov.

Sepala 5 rotundata basi coalita imbricata. Petala 5 libera ovato-oblonga praeefloratione cochleari vel contorta. Stamina 30 filamentis basi breviter coalitis. Antherae dorsifixae oscillantes connectivo oblongo crasso obtusissimo pistilato vel malleiformi, 2 thecis unilocularibus subglobosis ad basim dispositis, tantum 5-15 fertiles. Ovarium ovoideum 5-loculare loculis oppositisepalis uniovulatis, ovulis anatropis raphe ventrali. Stylus crassus brevis. Stigma 5-lobatum. Drupa grandis subfussiformis exocarpio crasso subfarinaceo. Endocarpium lignosum durum haud resinosum eminente 5-costatum profunde 5-sulcatum fundo sulcis operculo lineari costiformi dehiscenti instructo. Semina oblonga. Arbores foliis alternis coriaceis petiolatis persistentibus. Inflorescentiae cymoso-paniculatae axillares breves bracteatae bracteolataeque. Typus: *Sacoglottis heterocarpa* Ducke.

Sepals 5, suborbicular, imbricate, united at base. Petals 5, free, thick, oblong, the estivation cochlear or contorted. Stamens 30, glabrous, the filaments biseriate, conrescent at base, thick and papillose except toward the narrowed and pointed apex. Anthers only 5 to 15 fertile, dorsifixed, the connective thick, very obtuse, club or hammer shaped, the thecae 2, unilocular, subglobose, basal, dehiscing by the insertion line. Disk of 10, linear, thick, free scales. Ovary ovoid, strigose, 5-locular, the cells uniovulate. The carpels opposite the sepals. Ovules anatropous with ventral raphe, pendulous. Style thick, very short. Stigma subcapitate, 5-lobate. Drupe large, subfusiform, the exocarp thick, subfarinaceous. Endocarp woody, hard, not resinous, prominently 5-costate, the elevated ribs alternating with deep furrows, each having in the bottom a long linear germinal operculum protruding as one rib. Seeds oblong, usually only 1-2 (rarely 5) developed. Evergreen trees with simple alternate, coriaceous, petiolate leaves. Inflorescences axillary, dichotomous-paniculate. Bracts soon deciduous.

Hylocarpa differs from *Sacoglottis* in its large, compact (not resinose) narrow-valvate-dehiscent endocarp. From this and all other humiriaceous genera it further differs in its thick, obtuse, pistillate or hammer shaped anther-connectives bearing two basal unilocular glabrous thecae, and in having 30 stamens, of which only 5-15 may be fertile. Only one species of this genus is known, the Brazilian *Hylocarpa heterocarpa*. (See figs. 3, 16, and 18-19.)

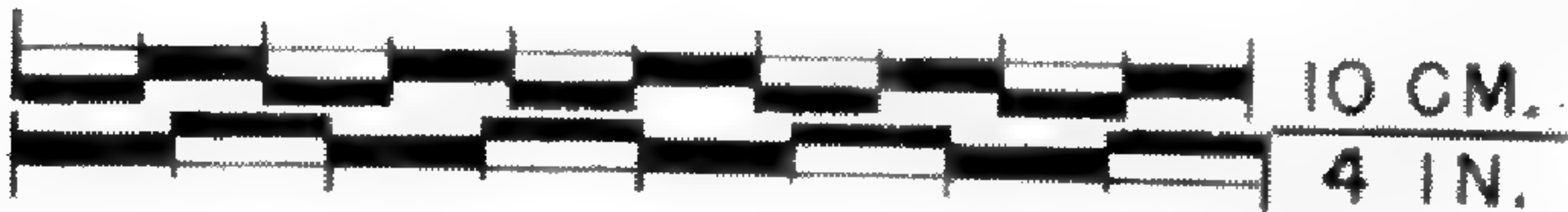
The name "*Hylocarpa*" is derived from the Greek "*hyle*" and "*hylo*" (wood), and *karpos*" (fruit), an allusion to the hard, woody large endocarp.



Vantanea compacta (Schniz.) Cuatr. (—*Humirium compactum* Schniz., —*Humirium contractum* Moric.; holotype, Blanchet 3362, P)



Funtanea compacta subsp. *microcarpa* Cuatr. (type, Pearce, K)



Vantanea guianensis Aublet

X-1958 Type collection

Vantanea guianensis Aubl. (type, Aublet, S)



Humiria balsamifera var. *floribunda* (Mart.) Cuatr. (= *Humirium floribundum* Mart.; type, Martius M)



Humiria balsamifera var. *guianensis* (Benth.) Cuatr. (= *Humiria cassiquiari* Sussenguth & Bergdolt; type, *Luetzelburg* 22627 and 22575, M)



Humiria balsamifera var. *parvifolia* (Juss.) Cuatr. (= *Humirium parvifolium* Juss.; type, St. Hilaire, P)



Humiria balsamifera (Juss.) Cuatr. (= Humirium arenarium Guillem.)
X 1957 (Guillemin)

W. G. MES. PARIS

Herb. Mus. Nat. Hist. Paris

Humiria balsamifera var. *parvifolia* (Juss.) Cuatr. (= *Humirium arenarium* Guillem.; type, Guillem. 205, P)



Ministerio de Agricultura y Cria
HERBARIO NACIONAL DE VENEZUELA
Humiria balsamifera (Willd.) A.H. var. *coriacea* Cuatr.

Num.
 Num. Col.
 Col.
 Fecha
 19

Humiria balsamifera var. *coriacea* Cuatr. (type, Cardona 1823, US)



Humiria balsamifera (Aubl.) V. Hil
var. *guaiquinimana* Cuatr.
X-98 H-2074 9

Humiria balsamifera var. *guaiquinimana* Cuatr. (type, Cardona 1112, US)



HERBARIUM OF
THE NEW YORK BOTANICAL GARDEN

PLANTS OF TERR. AMAZONAS, Venezuela

NO. 42760

Humiria wurdackii Cuatr. Holotype

Shrub 1-5 m. Fls white. Locally abundant at margins of Sabana Cumare on right bank of Caura Caura R16 Atabapo 20 km. above San Fernando de Atabapo, elev. 125 m.

THE NEW YORK BOTANICAL GARDEN

VOUCHERS FOR WOOD SAMPLES DEPOSITED
AT SYRACUSE AND YALE UNIVERSITIES

COLLECTED BY J.J. Wurdack & L.S. Adderley 3 June 1959

Humiria wurdackii Cuatr. (type, Wurdack and Adderley 42760, US)



Humiriastrum villosum (Fröes) Cuatr. (= *Sacoglottis villosa* Fröes; type, *Fröes* 22644, IAN)



Humiriastrum subcrenatum (Benth.) Cuatr. (*Humirium subcrenatum* Benth.; type, Martin, K)



R. & K. KRUKOFF'S 5th EXPEDITION TO SOUTH AMERICA

11270

Humiriastrum mapiriense
Cuatr.

112-58 Type fruit

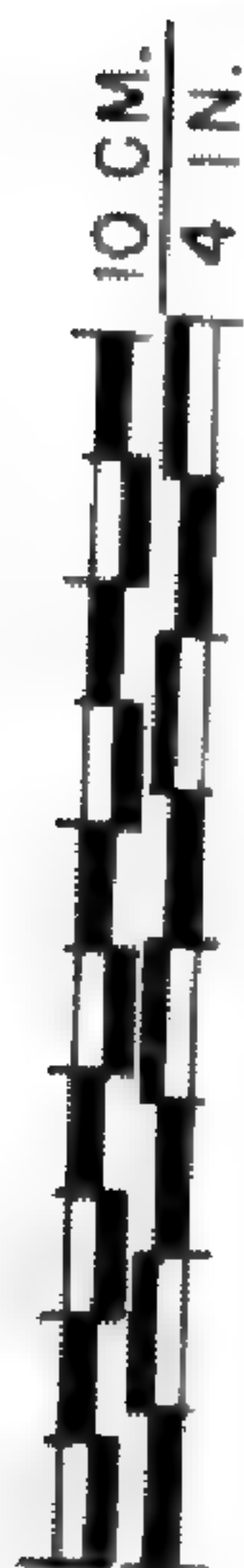
LEAFY BRANCH

BOLIVIA: Department of La Paz: Province of Ixcos: Copacabana (about 10 km. south of Mapari), alt. 850-950 m. Oct. 8-Nov. 15, 1939

Specimen distributed through the New York Botanical Garden

UNITED STATES NATIONAL MUSEUM

Humiriastrum mapiriense Cuatr. (type, Krukoff 11270, US)



COSTA RICA

STATES NATIONAL MUSEUM

Humiriastrum diguense subsp. *costaricense* Cuatr. (Allen 5812, US)



Schistostemon auyantepuyense
Cuatr.
X-1958 Holotypus

Ministerio de Agricultura y Cría
HERBARIO NACIONAL DE VENEZUELA
saccoglottis

Núm. 4061

Núm. Col 1st Col + Fect.

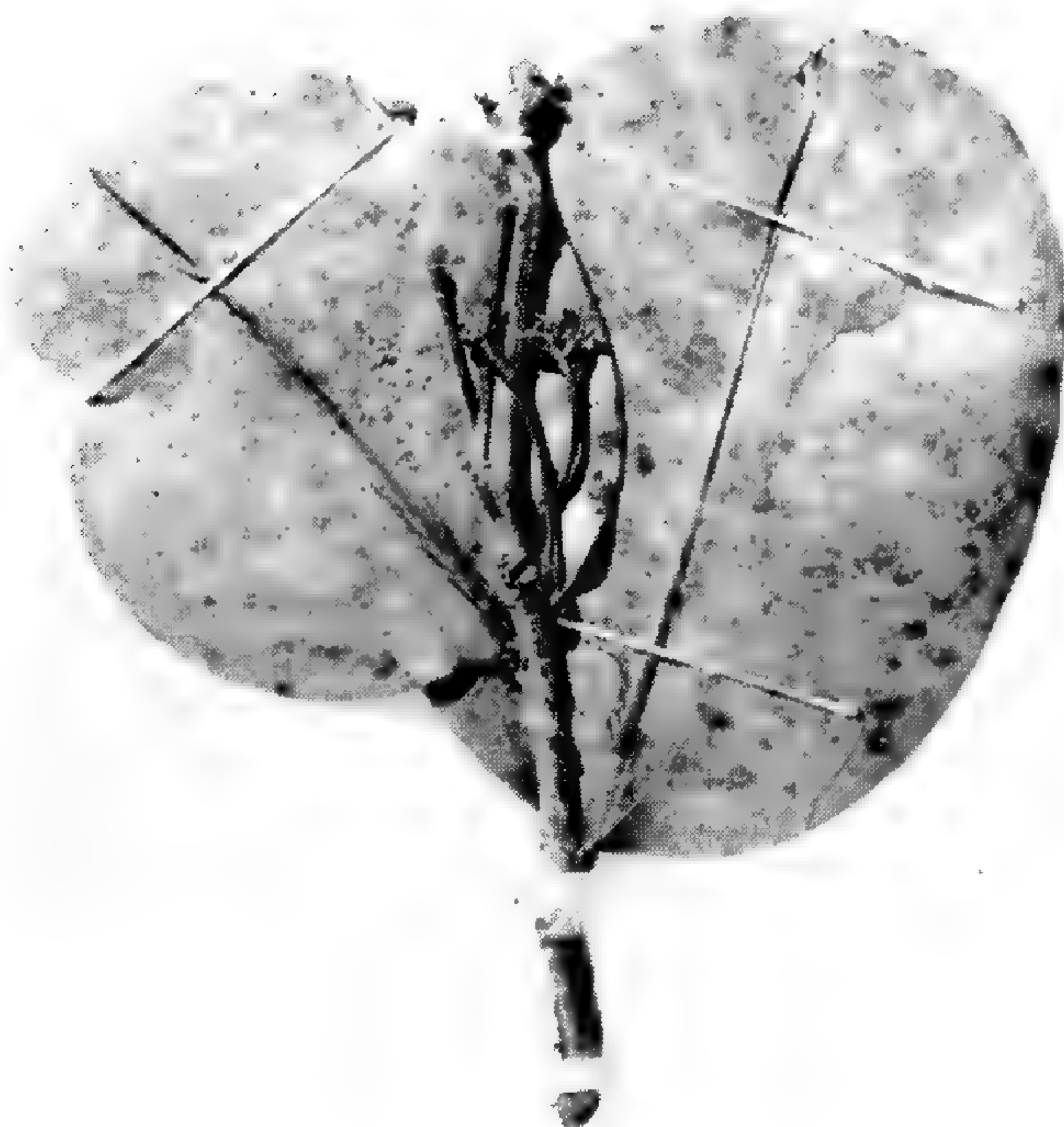
Schistostemon auyantepuyense Cuatr. (Vareschi & Foldats 4673, type, VEN)



Schistostemon reticulatum
subsp. *Froesii* Cuatr.
8-1958 Holotypus

PLANTAS DEL PARAGUAY

Schistostemon reticulatum subsp. *froesii* Cuatr. (Fróes 21370, NY)



Schistostemon retusum
(Ducke)
X-58 Isolippus



UNITED STATES NATIONAL MUSEUM

I. B. V.

JARDIM BOTANICO DO RIO DE JANEIRO
HERBARIO

No. 30131 Arb. N°
Fam. *Simarubaceae*
N. acut. *Sacoglottis retusa* Ducke n. sp.
Var.
Nome vulgar
Procedencia *do Rio de Janeiro, Serra da
Macula, Município de Parati, RJ*
Observações *det. Ducke*

Collect. *H. Ducke*

Determin. por *H. Ducke*

Date *2. 5. 52*

Date

Schistostemon retusum (Ducke) Cuatr. (= *Sacoglottis retusa* Ducke; type, Ducke 20131, US)



Sacoglottis duckei Huber
Holotypus

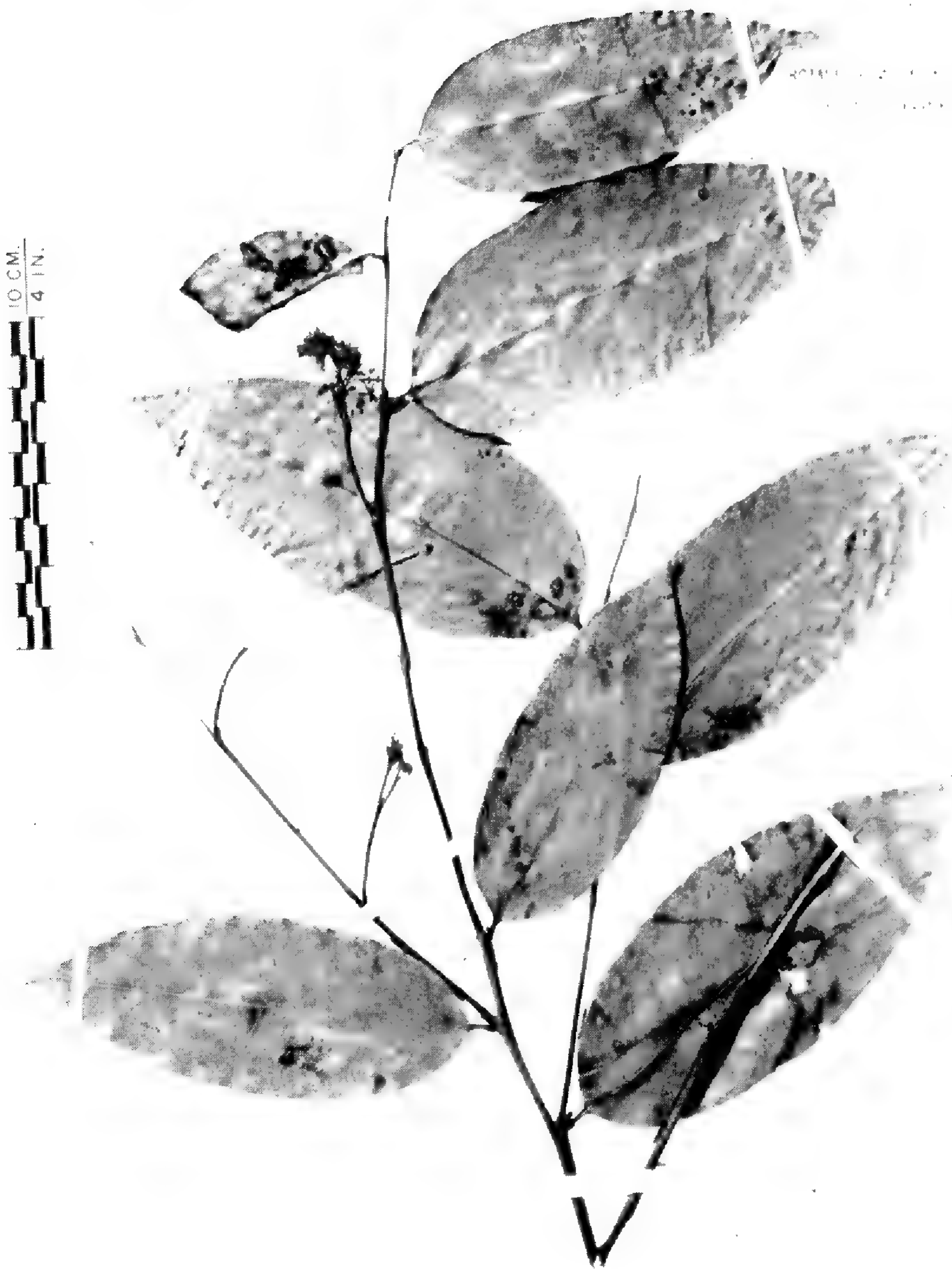
V-58

Schistostemon macrophyllum
(Benth.) Cuatr.

X-58



Schistostemon macrophyllum (Benth.) Cuatr. (*Sacoglottis duckei* Huber; type, Ducke 71711, MG)



Schistostemon densiflorum (Benth.) Cuatr. (= *Sacoglottis kaboeriensis* Bakh. f.; type, *Boschwezen* 2068 U)



Sacoglottis amazonica Mart. (Martius, M)



Sacoglottis guianensis fma. *guianensis* Benth. (Schomburgk 571, P)



Sacoglottis matogrossensis Malme
Holotype
= *S. quinensis* v. *pteroarpa* Drake
A-58

Malme Type Hb.

Herb. Brasil. Regnell. Mus. bot. Stockholm.
Plante linaire Remelland 11th No 223
Sacoglottis matogrossensis
Fig. 11.
Brasil: prov. Mato Grosso. St. Anna da Chapada.
10/8/22
reg. Gust. O. Silva Malme.

Sacoglottis matogrossensis fma. *matogrossensis* Malme (Malme 2237, type, S)



Sacoglottis mattogrossensis
var. *subintegra* (Ducke) Cuatr.
fma. *puberula* Cuatr. Holotype
det. J. Cuatrecasas XI-1958

Sacoglottis mattogrossensis
var. *subintegra* Ducke
18.5 fma. *puberula* Cuatr.

HERBARIUM AMAZONICUM MUSEI PARANENSIS (Museu Gald.)	
PARANÁ (BRASIL)	
Foliar	

Sacoglottis mattogrossensis Malme var. *subintegra* (Ducke) Cuatr. fma. *puberula* Cuatr.
(Ducke 16286, type, MG)



IX-115 17-1-47
HERB. ACAD. RHENO-TRAI

SURNAME Boschwezen (Forest Reserve)

Number (See Number)

Number of the Bureau van het boschwezen

Number of the Bureau van het boschwezen

Ruwa to balle
O. M. 61

Sacoglottis cydonioides Cuatr. (type, Boschwezen 6495, U)

1. *Hylocarpa heterocarpa* (Ducke) Cuatr., comb. nov.

FIGURES 16,l-p, 18,c; 19,a-c-

Sacoglottis heterocarpa Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 4:27, pl. 2. 1938.Type: *Ducke* 30137, Brazil, Amazonas, Rio Curicuriary.

Large tree with glabrous, more or less reddish terminal branchlets. Leaves large, thick-coriaceous, glabrous. Petiole 3-6 cm. long,

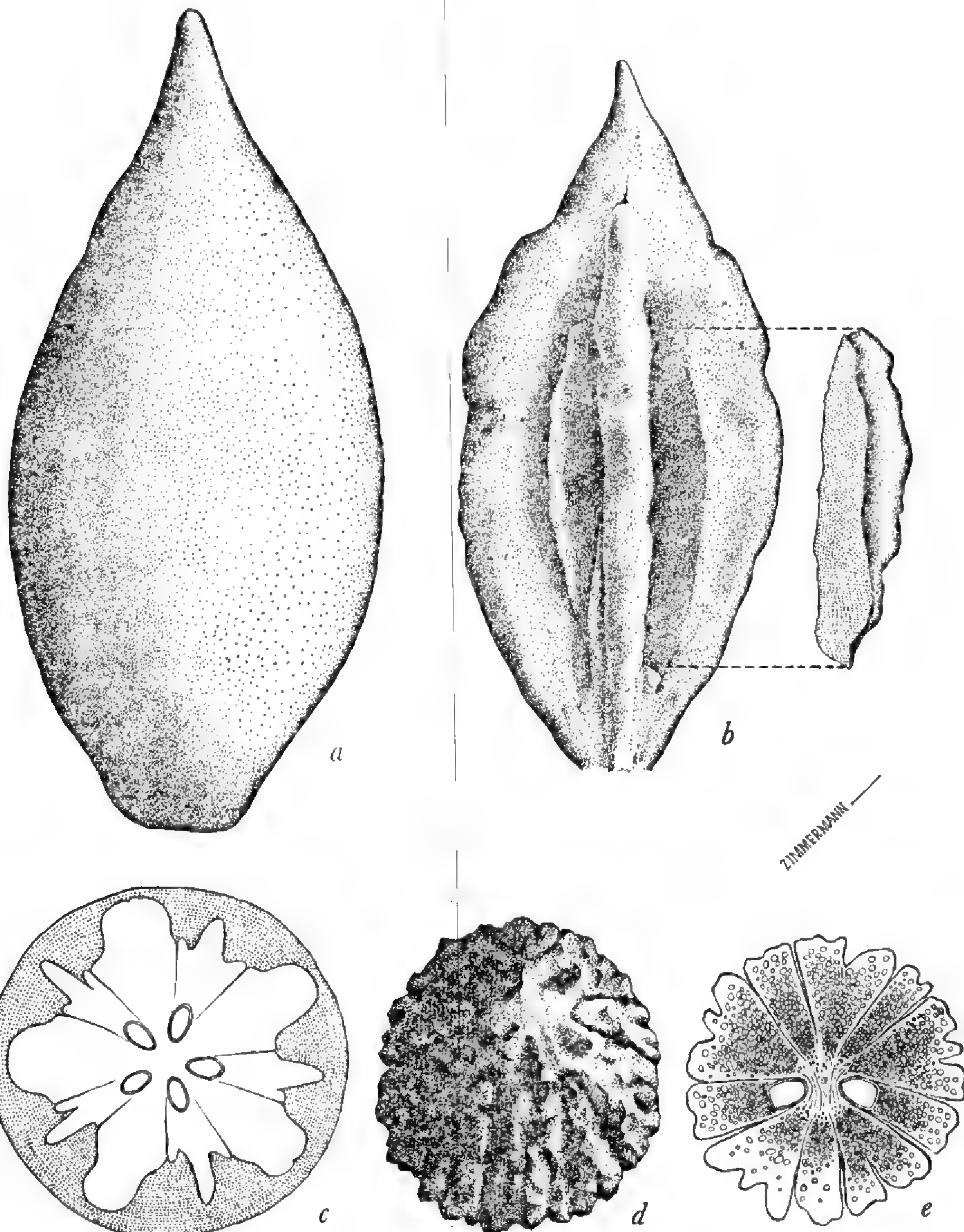


FIGURE 19.—a-c, *Hylocarpa heterocarpa*, $\times 1$ (*Ducke* 30137): a, fruit; b, endocarp showing a detached valve; c, transection. d-e, *Duckesia verrucosa* (*Ducke* 16764): d, endocarp, view from apex; e, transection (see two seeds).

semiterete, striate, sulcate above. Blade obovate-elliptic or sub-obovate, obtusely narrowed at base and decurrent along the petiole, rounded or very obtuse at apex, slightly crenate or subentire at margin, 11–17 cm long, 7.5–10 cm. broad; above, dark green or brownish, the midrib flat but conspicuous, the secondary nerves and veins more or less prominulous; beneath brown or reddish when dry, the midrib thick, striolate, the 14–16 pairs of secondary nerves thin and prominent, ascending, curved at their insertion, arcuate and anastomosing near the margin, the tertiary nerves and minor veins lax-reticulate, prominulous.

Inflorescences cymose-paniculate, shorter than the petioles, dichotomous; the short peduncle and the branchlets complanate, whitish-puberulous. Bracts ovate-triangular, ciliate, deciduous, the uppermost 0.5 mm. long. Pedicels 0.1–0.2 mm. long, glabrous, articulate with a short (0–0.5 mm.), hirtellous peduncle. Sepals 5, orbicular, united at base, ciliate at margin, glabrous outside, 0.8–1 mm. long. Petals 5, free, white, rather thick, linear-oblong, obtuse, glabrous, about 3.5 mm. long and 1.5–1.8 mm. wide, the estivation cochlear or contorted. Stamens 30, more or less biseriate, concrescent at base, the filaments 1.5–1.7 mm. long, rather thick, filiform at the end, broadening at the middle, densely covered with long papillas. Anthers dorsifixed, versatile, only 15 or less fertile; the connective carnose, oblong clavate or hammer-shaped, with 2 unilocular, globose, 0.7–0.8 mm. broad separated thecae at base; sterile anthers oblong, thick, obtuse at apex, 0.7–0.9 mm. long. Disk perigynous formed by 10 linear, thick, about 3 mm. high scales. Ovary ovoid, slightly 10-sulcate, strigose, 0.8 mm. long, 5-locular, the cells opposite the sepals, uniovulate. Style short, rather thick. Stigma 5-lobate. The ovules anatropous with ventral raphe. Drupe elliptic-subfusiform, about 9.5 cm. long, 4.5 cm. broad, attenuate toward the base, abruptly rounded-constricted at base, narrowed upward, apiculate, the apiculum about 1 cm. long, more or less curved. Exocarp smooth, 2–3 mm. thick. Endocarp woody, broadly fusiform, truncate at base (about 1 cm. diameter), middle part about 3.6 cm. in diameter, very narrow at apex and acutely apiculate, deeply 5-sulcate, 5-costate, the ribs very thick, prominent and robust, each of the 5 sulci with a germinal operculum or window in form of a 4 cm. long, very narrow, compressed rib, only 2–3 (rarely 5) fertile.

According to Ducke, the mature fruit of *H. heterocarpa*, called “cumate rana” by the natives, has an easily separable mesocarp, somewhat farinaceous, dry and tasteless. It is a tree of the catingas of the uppermost part of the Rio Negro basin at the Brazilian corner between Colombia and Venezuela.

BRAZIL: AMAZONAS: Rio Curicuriary, afluyente del rio Negro, in silva "catinga" circa Cataractam Cajú, loco paludoso; arbor sat magna, fructus virides, "cumatê da catinga," *Ducke* 265 (Isotypes, NY, Y). Same locality and data, flores, 18-XI-1936, fructus, 21-II-1936, *Ducke* 30137 (isotypes, US, U). Rio Içana, Tunuf, pé da serra, terreno pedregoso (arenito); arvore de 10-15 m., flor branca, 23-X-1947, *J. Murça Pires* 708 (IAN).

5. *Humiria*

Humiria St. Hil. Exp. Fam. 2:374. 1805.—Person, Syn. Pl. 2:70. 1807.—DC. Prodr. 1:619. 1824.—Benth. & Hook. Gen. Pl. 1:247, in part, 1862.—Urb. in Mart. Fl. Bras. 12(2):437, tab. 92. 1877.—Reiche in Engl. & Prantl, Pflanzenfam. 3(4):37, fig. 32. 1890.—Winkl. in Engl. & Harms, Pflanzenfam. 19a:106, fig. 59. 1931.—Lemée, Dict. Desc. Synon. Gen. Phan. 3:670. 1931.—Bakhuizen van den Brink in Pulle, Fl. Surin. 8(1):413. 1941.

Houmiri Aubl. Pl. Guian. 1:564, pl. 225. 1775.—Lam. Encycl. 3:139. 1789.

Wernisekia Scop. Intr. Hist. Nat. 273. 1777.

Myrodendrum, Schreb. Gen. Pl. (8 ed.), 1:358. 1789.

Houmiria Juss. Gen. Pl. 435. 1789.

Humirium Rich. ex Mart. Nov. Gen. Sp. 2:142. 1827.—Endl. Gen. Pl. 1040 (No. 5486). 1840.—Walp. Repert. Bot. Syst. 1:425. 1842.—Benth. in Hook. London Journ. Bot. 2:373 (in part). 1843.—Benth. in Hook. Journ. Bot. Kew Misc. 5:100 (in part). 1853.—A. Juss. in St. Hil. Fl. Bras. Merid. 2:88. 1829.—Muell. in Walp. Ann. Bot. Syst. 4:383 (in part). 1857.—Baill. Adansonia 1:209. 1860; 2:262-264. 1861.

Myrodendron Spreng. Syst. Veg. 2:600. 1840.

Verniseckia Steud. Nom. Bot. (2 ed.), 2:752. 1841.

Houmiri Sect. *Humirium* Baill. Adansonia 10:370 (in part). 1873.—Hist. Pl. 5:54, figs. 88, 89 (in part). 1874

Wernischeckia Scop. ex Post & Kuntze, Lexicon 288. 1904.

Type species: *Humiria balsamifera* (Aubl.) St. Hil.

Sepals 5, suborbicular or ovate, imbricate, more or less coalescent in a cupular calyx. Petals 5, free, thick-membranaceous, oblong or linear, subacute or obtuse, the estivation cochlear or quincuncial. Stamens 20, uniseriate, the filaments united in tube on about the lower half, more or less complanate, densely papillose or muricate, 10 longer and alternating with the shorter 10. Anthers ovoid-lanceolate, dorsifixed above the base, the connective thickly linguiform or lanceolate, much longer than the 2 subglobose, hairy thecae inserted sublaterally on the inside at the base, opening when pulled away. Disk annular, surrounding the ovary, formed by 20 linear, thick, more or less united scales. Ovary scarcely pilose at apex or completely glabrous, 5-locular (rarely 4-locular), each cell with 2 anatropous, pendulous, superposed ovules. Carpels opposite the petals. Style columnar, erect, as long as the filaments or longer, more or less hirsute. Stigmas globose, stellate. Drupe small (not exceeding 16 mm.), ovoid, ellipsoid or oblong; the epicarp thin; the mesocarp fleshy, usually more or less sweet and aromatic, edible. Endocarp

woody, ellipsoid or ovoid, finely 10 (rarely 8) striate; the striae equidistant marking 5 longitudinal, narrow, germinal valves, alternating with 5 small holes at the apex; each cavity of the ovary usually developing into 2 superposed cavities with 1 seed in each; sometimes the 2 superposed seeds and cavities present and fertile; at other times only 1 cavity (generally the lower one) fertile; often the inferior fertile one alternating with the next superior one; usually 1-4 seeds fertile, rarely more. Although no written material exists about the dehiscence and germination of *Humiria* fruits, their structure makes me assume that at the moment of germination, the narrow valve is pushed away by the pressure of the embryo. Seeds commonly 4-1, well developed, 3-5 mm. long, subpyriform-ellipsoid, oblong, acute at apex, the outer episperm scaly, the inner membranaceous; the endosperm carnose. Evergreen trees or shrubs; wood hard. Leaves alternate coriaceous or subcoriaceous, sessile or petiolate, often more or less decurrent on the branchlets; margin slightly crenate rarely completely entire, dotted with glands near the margin on the lower side. Stipules small, falling soon or lacking. Inflorescences paniculate and corymbiform with apparently alternate branching or dichotomous, axillary or subterminal. Bracts persistent. (See figs. 3 and 20-23.)

There are only three recognized species of *Humiria* in this treatment; one of them with numerous varieties and forms is widely spread through the rain forests and savanna thickets of tropical South America. They are important constituents of the above communities and may become dominant in bush or thicket communities in savannas and on the Guiana sandstone hills.

The name, "Humiria" is taken from the Caribbean name "umiri," given in French Guiana for *H. balsamifera* and is the form conserved by the Code of International Nomenclature (see page 33).

Key to the Species of *Humiria*

1. Leaves small or linear.
 2. Leaves linear (2.5-10×0.3-0.8 cm.), glabrous. Plant entirely glabrous. Sepals orbicular, very obtuse **3. *H. wurdackii***
 2. Leaves small (1.5-4×0.5-1.5 cm.), oblong or elliptic-oblong, minutely patulous-pilose, slightly velutinous at both sides, sessile. Young branchlets minutely pilose. Sepals subacute **2. *H. fruticosa***
1. Leaves larger, glabrous or only the midrib pubescent beneath, rarely the blade sparsely hirtellous. Sepals orbicular or very obtuse.
 3. Leaves broad (7-14×4-9.5 cm.); blade thick-coriaceous, rigid, oblong-obovate or obovate-elliptic; petiole stout, broadly winged, folded-amplexant. Drupe ellipsoid, 10-12 × 7-9 mm. Plant entirely glabrous. **4. *H. crassifolia***
 3. Leaves medium-size (4-12×2-6 cm.), small (1.5-5×0.8-2.5 cm.), rarely larger (up to 18 cm. long); blade subcoriaceous or coriaceous, sessile and

amplectant or petiolate; petiole flat, narrower, not amplexant. Drupe oblong-ellipsoid or oblong, 10–14×4–8 mm. Plant glabrous or somewhat pubescent 1. *H. balsamifera*

1. *Humiria balsamifera* (Aubl.) St. Hil., Exp. Fam. 2:374. 1805.—Urb. in Mart. Fl. Bras. 12(2):440, tab. 92, fig. I. 1877. DC. Prodr. 1:619. 1824.

FIGURE 20; PLATES 4–9

- Houmiri balsamifera* Aubl. Pl. Guian. 1:564–566 pl. 225. 1775.
Myrodendrum balsamiferum Raeuschel, Nom. Bot. (3 ed.) 156. 1797.
Myrodendrum amplexicaule Willd. Sp. Pl. 2(2):1171. 1800.
Myrodendron amplexicaule Spreng. Syst. veg. 2:600. 1825.
Humirium floribundum Mart. Nov. Gen. Sp. Pl. 2:143–145, pl. 199. 1827.—
 Benth. in Hook. Lond. Journ. Bot. 2:374. 1843.—Benth. in Hook. Journ. Bot. Kew Misc. 5:100. 1853.
Humirium montanum A. Juss. in St. Hil. Fl. Bras. Merid. 2:90. 1829.
Humirium parvifolium A. Juss. in St. Hil., ibid.:89. 1829.
Humirium parviflorum A. Juss. in St. Hil., ibid.:63. 1829.
Humirium guianense Benth. in Hook. London Journ. Bot. 2:374. 1843.—
 Hook. Journ. Bot. Kew Misc. 5:100. 1853.
Humirium balsamiferum Benth. in Hook. Journ. Bot. Kew Miscel. 5:102. 1853.
Humirium surinamense Miquel, Stirp. Surinam 86, pl. 24. 1850.
Humirium arenarium Guill. in Baill. Adansonia, 1:208. 1860.
Humirium multiflorum Mart. Spach Suites 17 in Pritz. Icon. Bot. Ind. 560. 1866.
Houmiri arenarium Baill. Hist. Pl. 5:52–53, figs. 88–89. 1874.
Humiria floribunda Mart. ex Urb. in Mart. Fl. Bras. 12(2):438, pl. 92. 1877.—Ducke, Arch. Jard. Bot. Rio Janeiro 3:176. 1922.
Myrodendron petiolatum Mart. ex Urb. in Mart. Fl. Bras. 12(2):438. 1877, as synonym.
Humirium amplexicaule Mart. ex Urb., ibid.:440, as synonym. 1877.
Humirium ellipticum Klotsch ex Urb., ibid.:438, as synonym. 1877.
Humirium laurinum Klotsch ex Urb., ibid.:439, as synonym. 1877.
Humirium subsessile Spruce ex Urb., ibid.:439, as synonym. 1877.
Humiria Cassiquiari Süssenguth & Bergdolt, Repert. Sp. Nov. Fedde 39:16. 1935.
Humiria savannarum Gleason in Bull. Torrey Club. 58:378. 1931.
Humiria pilosa Steyermark, Fieldiana, Bot. 28:270. 1952.
Humiria floribunda var. *guianensis* (Benth.) Urb. in Mart. Fl. Bras. 12(2):439. 1877.
Humiria floribunda var. *laurina* Urb. in Mart., ibid.
Humiria floribunda var. *montana* (Juss.) Urb. in Mart., ibid.:438. 1877.
Humiria floribunda var. *parvifolia* (Juss.) Urb. in Mart., ibid.
Humiria floribunda var. *subsessilis* Urb. in Mart., ibid.:439. 1877.
Humiria floribunda var. *spathulata* Gleason, Bull. Torrey Club. 58:374. 1931.

Type: *Aublet*, French Guiana.

Small or large tree, in some varieties a low shrub. Branchlets hirtellous, puberulous or glabrous, more or less compressed, the very young in the typical form ancipital and more or less winged by decurrence of the leaf base, in other forms subterete. Leaves subcoriaceous or coriaceous, thin or thick, flexible or more usually rigid,

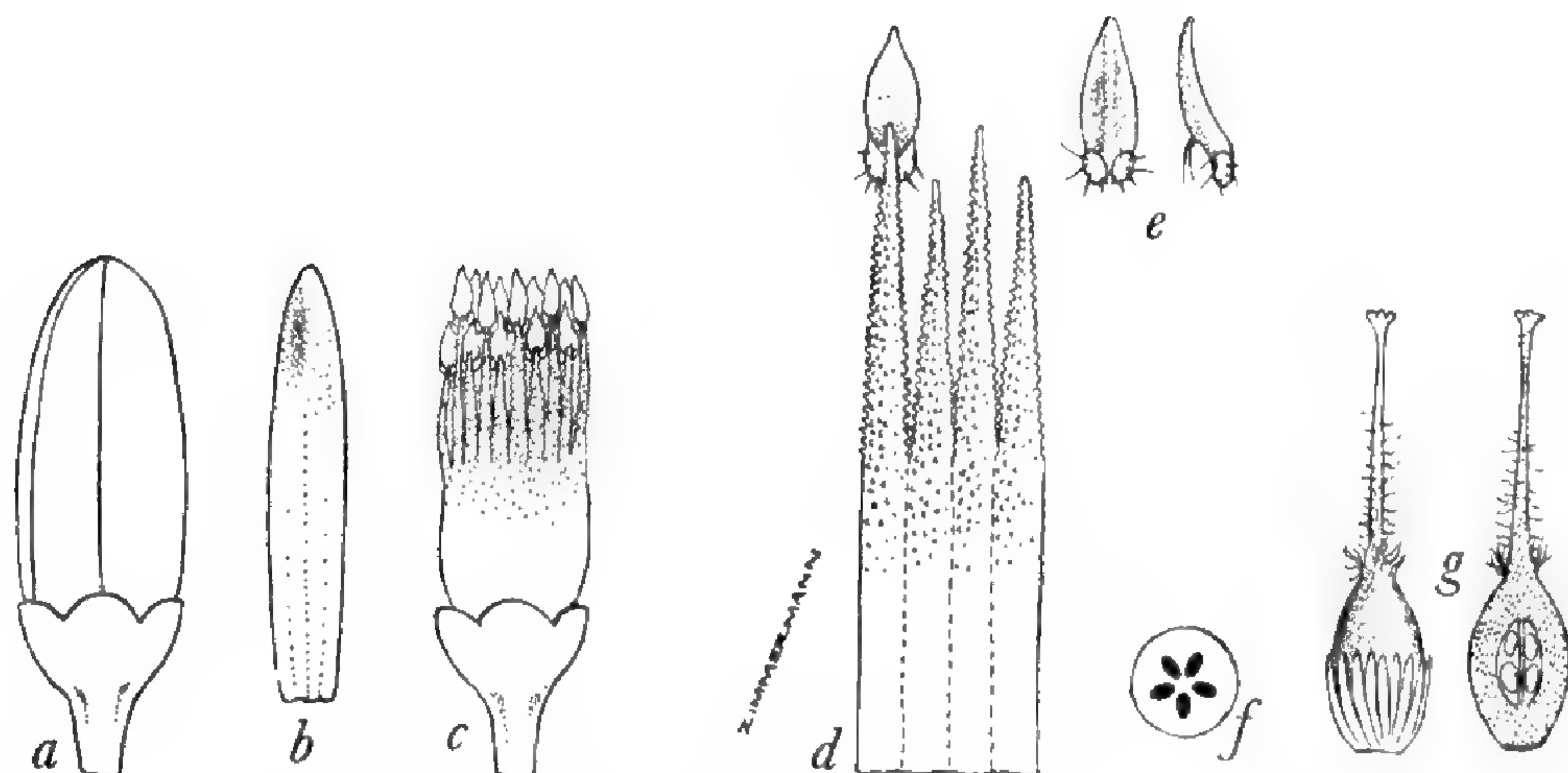


FIGURE 20.—*Humiria balsamifera* (Ducke 23424): *a*, bud, $\times 5$; *b*, petal, $\times 5$; *c*, flower, the petals removed, showing the androecium, $\times 5$; *d*, detail of staminal tube from the outside, $\times 10$; *e*, anther, $\times 10$, front and lateral view; *f*, ovary, transection, $\times 5$; *g*, gynoecium, from outside surrounded by the disk, and longitudinal section, $\times 5$.

sessile, subsessile or pseudopetiolate. Blade elliptic, obovate or oblong with variable shapes; in the typical form broad and amplexant at base, in others more or less attenuate at base, obtuse and sessile or cuneate and short-petiolate or abruptly contracted into a winged petiole; the apex rotundate, truncate or obtuse, broad or slightly attenuate, sometimes mucronulate, often emarginate and mucronate in the depression; very variable in size, up to 18 cm. long and 7 cm. broad. Glabrous above or rarely with hirtellous-puberulous, conspicuous midrib, lateral nerves slightly apparent; with prominent, glabrous or hirtellous midrib beneath, secondary nerves spreading, thin, slightly prominent and conspicuous, 3–5 mm. distant, curved and anastomosing near the margin, minor nerves parallel and others laxly reticulate.

Inflorescences axillary and subterminal, cymose-paniculate, usually corymbiform, 3–10 mm. long, very often aggregate forming very floriferous compound panicle; peduncle 1.5–6 cm. long, ancipital and winged in typical forms or simply angulate; branchlets rather stout, rigid, fastigate, often ancipital and more or less winged, thinner and subdichotomous above, more or less densely hirtellous or glabrous. Bracts triangular or ovate, 0.5–3 mm. long, amplexant. Pedicels 0.5–2 mm. long, thick, glabrous or rarely hirtellous, articulate with usually puberulous, rigid, 1–2 mm. long peduncles. Calyx cupular, 1–2 mm. high, the sepals rather thick, suborbicular, imbricate, lower part united, margin ciliolate, glabrous, rarely hirtellous outside. Petals cochlear or quincuncial in estivation, rather thick, white or greenish white, glabrous or rarely puberulous outside, lanceolate-linear, subacute or subobtuse at apex, 4.5–7 mm. long, 1–1.6 mm. broad. Stamens 20, filaments erect, rigid, 4–5 mm. long, alternating 2 sizes, united in lower half, free portion abundantly papillose. An-

thers ovate-lanceolate, 0.8–1 mm. long, thecae basal, subglobose, pilose. Disk annular with about 20 linear, glabrous scales united at base. Ovary ovoid, glabrous except for few hairs at apex, 5-locular, cells biovulate with superimposed ovules. Style erect, rather thick, more or less hirtellous, but glabrous near apex. Stigmas 5, thick, stellate-capitate. Drupe oblong-ellipsoid, 10–14 mm. long, 5–8 mm. thick, exocarp carnose, glabrous. Endocarp woody, ellipsoid-oblong, obtuse or rounded at base, attenuate and acute at apex with 5 very conspicuous foramina around tip; 10 thin and curved furrows longitudinally; showing in transection 5 irregular cells. Seeds variable in number, few.

H. balsamifera is a broad specific complex that includes a great number of different types with all possible transitional forms. Some of the extreme forms already have received specific denominations, such as *H. floribunda*, *H. guianensis*, *H. montana*, and *H. parvifolia*. In the "Flora Brasiliensis," Urban, understanding the great polymorphism of this group, merged the four species into one (*H. floribunda*) and recognized in it six varieties. Through the study of the abundant material, I came to the conclusion that all these varieties are variations of the basic form of *H. balsamifera*; furthermore, several new varieties, mostly endemics, have been discovered in recent expeditions, especially in the Guianan highlands.

The most important variations observed in *H. balsamifera* are concerned with the shape and size of the leaves and the indument. The leaf blades vary from sessile and amplexant (broadly auriculate) to narrowed and long petiolate, from obovate and subrotund to oblong, and from abundantly pubescent on the nerves beneath to glabrous; the leaf blades vary from thin-subcoriaceous to thick and rigid-coriaceous, from small (2–4 cm.) to large (up to 18 cm. long), and from an entire to finely crenulate margin. The young branchlets in the typical *H. balsamifera* are appressed, ancipital, and winged, but in other forms the young branchlets become angulate or subterete; they vary from completely glabrous to hirtellous. The fruit also varies from ellipsoid to ellipsoid-oblong. The auriculate, amplexant long leaves are a juvenile form; examination of abundant collections taken from the same tree at different times shows how this character changes. Surinam material from the Forest Service, which is rich in specimens taken from the same trees, shows the little value of the form that I call *attenuata* because specimens with broad auriculate amplexant leaves as well as with attenuate leaf blades are found on one single tree. Between the extreme forms given as types of varieties, all possible gradations are found.

The typical *H. balsamifera* has sessile and amplexant, obovate or elliptic leaves and winged young branchlets; an adult form with atten-

uate leaves at base is frequent (fma. *attenuata*). When the leaves are narrowed toward the base to being almost or shortly petiolate, we have the variety *floribunda* with usually wingless branchlets. The typical variety *guianensis* has obovate or broadly elliptic leaves, abruptly contracted into a petiole. When the blades are oblong and suddenly petiolate, we have the variety *laurina*. Other varieties are *savannarum*, with narrow sublanceolate leaves, attenuate at base; *parvifolia*, with small, obovate, attenuate-cuneate leaves; *coriacea*, with thick, rigid, obovate or elliptic-obovate leaves, attenuate at base; *guaiquinimana*, being like the former but with suborbicular and subsessile leaves; *stenocarpa*, differing in its thinner drupes and endocarps; *iluana*, differing from *coriacea* in its hirtellous petals; *imbaimadaiensis*, with its sessile, amplexant, elliptic leaves; *pilosa*, with more or less pubescent branchlets and leaves; and *minarum*, with a distinct subacute form of elliptic leaves.

Among the many reported names which are locally or regionally applied to *Humiria balsamifera* and varieties, the most common and widely used are "umiri" or "umiry," in Brazil and French Guiana, and "blakkaberie" or "blaka-berie" in Surinam.

Key to the Varieties of *Humiria balsamifera*

1. Leaves sessile or subsessile, broad and amplexant, or broadly attenuate at base.
 2. Leaves elliptic, rounded at both ends, amplexant at base, rigid-coriaceous, 2.5-5×1.7-3.2 cm. Branchlets subterete. . . . **lk. var. imbaimadaiensis**
 2. Leaves slightly attenuate toward the base, subrigid or flexible.
 3. Leaves broad toward the apex, obovate or obovate-elliptic, rounded or very obtuse at apex; 6-14×2.5-6 cm. Young branchlets flattened and more or less winged. **la. var. balsamifera**
 4. Leaves broad at base, more or less auriculate, amplexant.
 4. Leaves broadly attenuate, subcuneate at base. . . **la(1). fma. balsamifera**
 4. Leaves broadly attenuate, subcuneate at base. . . **la(2). fma. attenuata**
 3. Leaves narrowed toward the obtuse apex. Branchlets angulate or subterete, rarely narrow-winged.
 5. Leaves rhombo-elliptic-oblong or sublanceolate-elliptic, slightly attenuate, obtuse or rarely auriculate-amplexant at base, 3.5-10×1.5-4 cm. **lc. var. subsessilis**
 5. Leaves linear-oblong or subelliptic-oblong, sublanceolate, narrowed and subacuminate, attenuate-cuneate at base; 5-10×1.5-3.5 cm.
 - lf. var. **savannarum**

1. Leaves more or less attenuate at base with petiole or pseudopetiole.
6. Leaves abruptly contracted into a long, winged petiole, subcoriaceous or subrigid-coriaceous.
 7. Leaf blades broadly obovate or oblong-obovate or elliptic or suborbiculate, 3-12×2-6 cm. The midrib generally pubescent beneath. Pseudopetiole 0.5-2.5 cm. long. **ld. var. guianensis**
 7. Leaf blades elliptic-oblong, 3.5-7×1.5-3 cm., glabrous. Pseudopetiole 0.5-1.5 cm. long. **le. var. laurina**
6. Leaves gradually attenuate at base, more or less cuneate or suddenly cuneate-contracted with short (1-3 mm.) petiole.
 8. Leaves obovate or obovate-elliptic or rarely oblong-elliptic, long-attenuate, cuneate at base.
 9. Leaves medium-sized or large, 5-12×2-6 cm., subcoriaceous or subrigid-coriaceous. **lb. var. floribunda**
 9. Leaves smaller, 1.5-7 cm. long.
 10. Leaves subcoriaceous 1.5-4×0.8-2.5 cm., the veins slightly prominulous. Young branchlets angulate, hirtellous-puberulous. **lg. var. parvifolia**
 10. Leaves thick-coriaceous, rigid or subrigid, the veins prominulous especially beneath. Young branchlets glabrous or minutely hirtellous-puberulous.
 11. Petals hirtellous. Branchlets glabrous. Leaves 3.5-7×1.8-4 cm. Petiole 5-7 mm. **ll. var. iluana**
 11. Petals glabrous.
 12. Drupe oblong-ellipsoid, 10-14×5-8 mm. Leaves thick-coriaceous, 4-7×2.4-5.2 cm. Petiole 2-6 mm. Young branchlets hirtellous or glabrous. **lh. var. coriacea**
 12. Drupe oblong, 11-14×4-5 mm. Leaves thin-coriaceous 3-5.5×2-3.6 cm. Petiole 5-7 mm. Young branchlets glabrous. **lj. var. stenocarpa**
 8. Leaves generally subelliptic, short-attenuate at base, the veins prominulous beneath.
 13. Leaves suborbicular-elliptic or suborbicular, suddenly cuneate-attenuate in a thick, broad, short (about 2 mm. long) petiole; the margin usually entire, almost eglandular; 4-7×3-5.2 cm. Young branchlets hirtellous. **li. var. guaiquinimana**
 13. Leaves oblong-elliptic, slightly attenuate at both ends, thin-coriaceous, rather rigid, 3-5×1.5-2.5 cm.
 14. Leaves glabrous, attenuate, subacute or subobtuse at apex, narrowed at base with 1-2 mm. long petiole, the margin crenulate, gland-dotted beneath. Young branchlets glabrous. **ln. var. minarum**
 14. Leaves hirtellous on the midrib beneath, subrotund or subobtuse at apex, attenuate at base with 2-3 mm. long petiole; the margin generally entire, sometimes glandular. Branchlets hirtellous. **lm. var. pilosa**

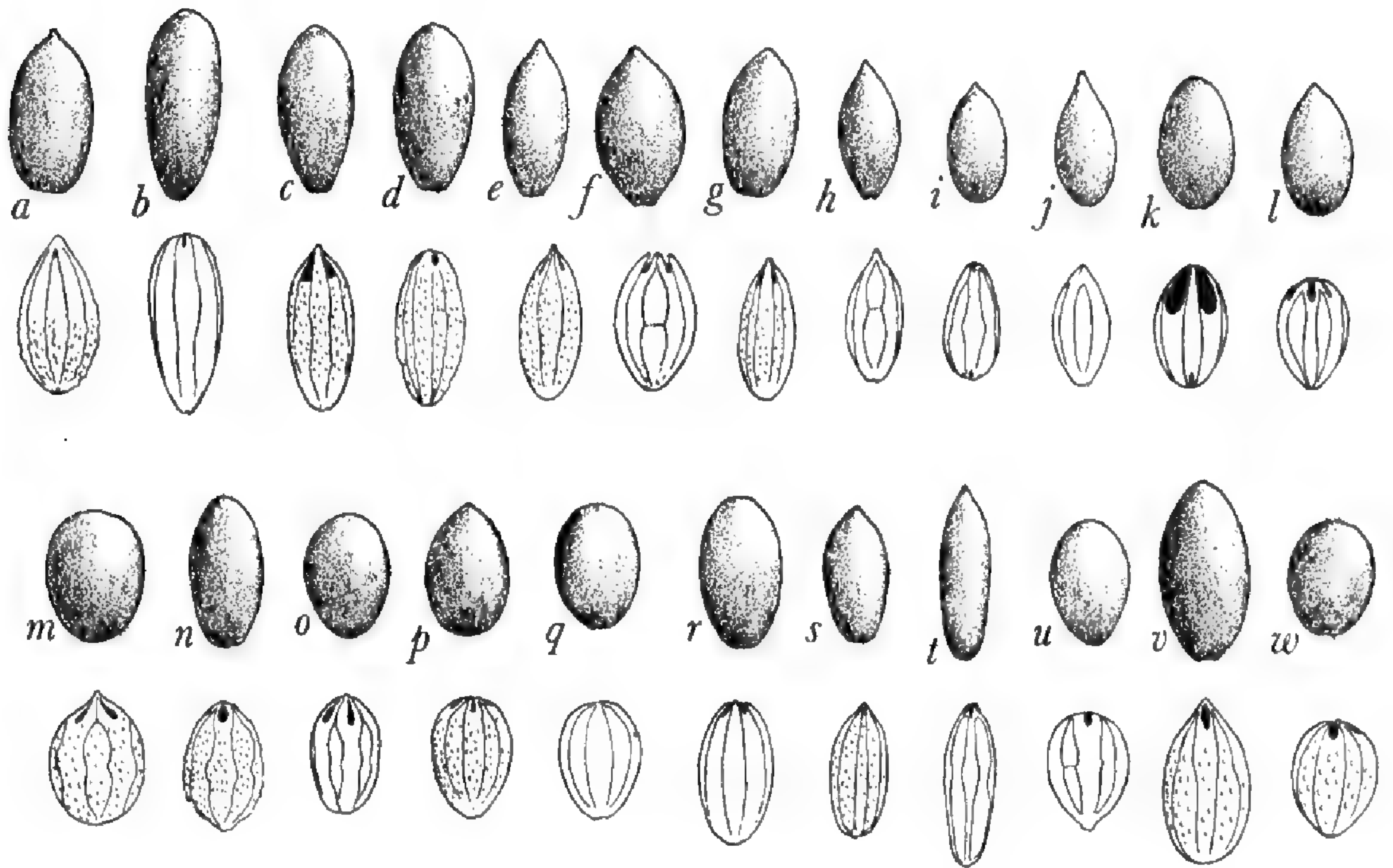


FIGURE 21.—a-t, *Humiria balsamifera*, $\times 1$, fruit and endocarp: a, var. *balsamifera* (Black 49-8369); b, fma. *attenuata* (Fróes 22738); c, fma. *attenuata* (A. C. Smith 2423); d, var. *floribunda* (Black 47-1756); e, var. *floribunda* (Maguire et al. 30987); f, var. *floribunda* (Maguire & Maguire 35040); g, var. *attenuata* (Maguire & Stahel 24957); h, var. *guianensis* (Maguire & Stahel 23654); i, var. *guianensis* (Maguire & Politi 28828); j, var. *laurina* (Maguire et al. 37632); k, var. *subsessilis* (Spruce 2454); l, var. *subsessilis* (Cowan & Wurdack 31472); m, var. *subsessilis* (Schultes & Lopez 9510); n, var. *subsessilis* (Williams 13868); o, var. *coriacea* (Maguire 24707); p, var. *coriacea* (Maguire & Politi 27627); q, var. *coriacea* (Maguire & Politi 27695); r, var. *coriacea* (Maguire et al. 30018); s, var. *stenocarpa* (Maguire et al. 35882); t, var. *stenocarpa* (Maguire & Maguire 40105); u, *H. crassifolia* (Maguire & Fanshawe 23233); v, *H. balsamifera* var. *savannarum* (Wurdack & Monachino 41380); w, *H. balsamifera* var. *guaiquinimana* (Maguire 32763).

1a(1). *Humiria balsamifera* var. *balsamifera* fma. *balsamifera*

FIGURES 21,a; 22,a-c

This variety is widespread throughout the savannas of British Guiana, Surinam, French Guiana, and the Brazilian States of Amazonas, Rio Branco and Pará, and is relatively common in wet and inundatable places.

BRITISH GUIANA: Mazaruni Station, tree 60 ft., 12 in. diameter with spreading crown on flat white sand areas by savanna; ripe fruit black, oval, edible, glossy, pulp sweetish; "tauaranzu," 10-I-1942, *Fanshawe* F715 (NY, U). Demarara River "Jouranaro," V-1887, *Jenman* 3912 (K, NY). Kartabo, small tree, clearing in second growth, 17-VIII-1920, *Bailey* 115 (GH). Essequibo River, Moraballi Creek near Bartica, near sea-level, "tauroniro" or "twaranru," tall tree, 121 ft. high, 3½-4 ft. diameter in Wallaba forest, bark thinly fluted, internodes winged, 5 white petals, numerous united stamens in column (compared with Aublet's specimens at B. by Sandwith), 8-X-1929, *Sandwith* 399 (NY, U, US, P). Rupununi River, Quimatta, X-1889, *Jenman* 5672 (K). Without locality, *Rudge* s.n. (BM).

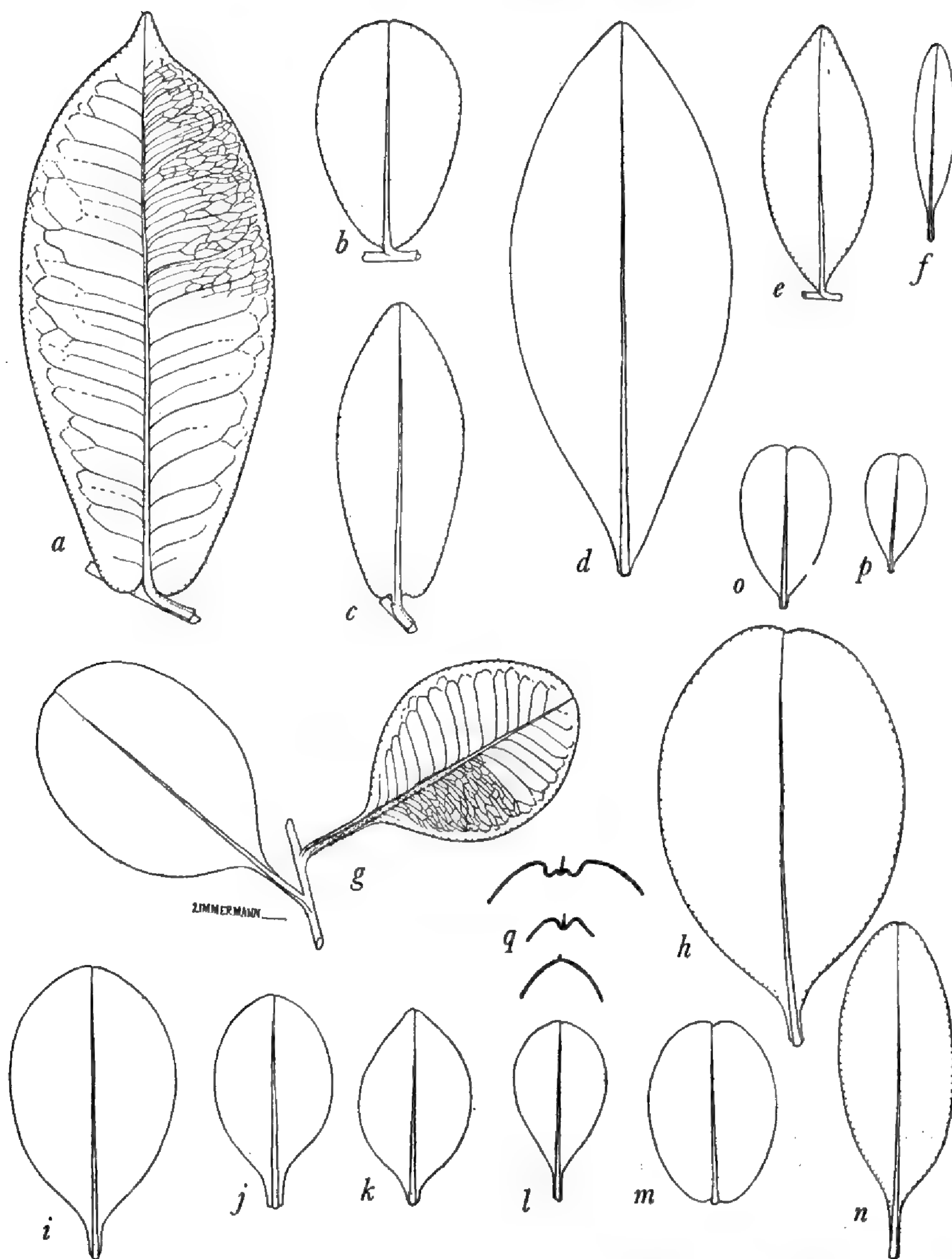


FIGURE 22.—*Humiria balsamifera*, leaves: *a*, var. *balsamifera* (Herb. Richard, French Guiana); *b*, var. *balsamifera* (French Guiana); *c*, var. *balsamifera* (French Guiana); *d*, fma. *attenuata* (Schultes & Cabrera 15511); *e*, var. *subsessilis* (Spruce 2454); *f*, var. *laurina* (Maguire et al. 36354); *g*, var. *guianensis* (Schomburgk 270); *h*, var. *guianensis* (Maguire et al. 41917); *i*, var. *coriacea* (Maguire & Fanshawe 23295); *j*, var. *coriacea* (Cardona 1869); *k*, var. *coriacea* (Maguire & Politi 27627); *l*, var. *coriacea* (Maguire 24443); *m*, var. *imbaimadaiensis* (Maguire & Fanshawe 32158); *n*, var. *laurina* (Schomburgk 560); *o*, var. *parvifolia* (St. Hilaire, “*H. montanum*”); *p*, var. *parvifolia* (St. Hilaire); *q*, different types of mucronate tip in *H. balsamifera*, especially in var. *coriacea*.

SURINAM: Boschreserve Brownsberg, Boomnummer 1273, 20-X-1924, *Boschwezen* 6670 (U); 21-VII-25, *Boschwezen* 6907 (U). Savannah near Bownsweg, tree, "blakkaberie," 13-XI-1933, *Lanjouw* 1253 (US, U). Boschreserve Zanderij I, *Boschwezen* 6234 (U). Zanderij I, Boomnummer 39, *Boschwezen* 1547, 2765, 2885, 5827 (U); 1935 (U, IAN, US); 2232 (U, US); 3010 (IAN, U). In maurisie moerasbos op veen langs kreek in savanne bos bij Zanderij I; boompje, "swietmerie" (Sur), 28-VIII-1954, *Lindeman* 6541 (U). Boschreserve Sectie O, Boomnummer 92, *Boschwezen* 4669 (U, IAN); Boomnummer 845, *Boschwezen* 2471, 2918, 3934, 4684, 4810, 5412, 5858, 6010, 6068 (U). Zandsavanne W van Patamacca, 23-I-1949, *Lanjouw & Lindeman* H8 (U). Blakawaka, 2-II-1921, *Junker* 5525 (U). Jodensavanne high savanne side forest, sandy soil, alt. 70 ft., 16-V-1954, *Houtmonster* 543A (Y); low forest, soil clay, 70 ft., 15-V-1954, *Houtmonster* 541A (Y); 15-V-1954, *Houtmonster* 542A (Y). Jodensavanne-Mapane kreek area (Suriname R), op droge zandsavanne bij Blakawatra kreek, struik, "blaka-berie" (Sur.), 17-XII-1954, *Lindeman* 6880 (U); op droge zandsavanne aan Blakawatra kreek; hoge struit, 17-XII-1954, "blakaberie" (Sur.), *Lindeman* 6861 (U); op droge zandsavanne achter Suhoza, struikje 2 m. hoog, 10-VII-1953, *Lindeman* 4202 (U). Patricksavanne, 9-V-1910, *Boschwezen* "Indig." 212 (U). Via secta ab Moengo tapoe ad Grote Zwiebelzwamp; Kleisavanne O van km. 65, struik 1.25 m. hoog; vrucht onrijp, groen, "blakaberie" (Sur.), "tawararo" (Arow), 29-IX-1948, *Lanjouw & Lindeman* 573 (U); km. 6.7, struik 2½ m., bloem wit, *Lanjouw & Lindeman* 652 (U). Wajombo R., Donderkreek, op Zandsavanne; kleine boom circa 8 m. hoog, over de geheele stam dicht begroeid met donkergroen loof met eigenaardigen boomvorm, "tawaanroe" (Arow), "meerie" (Kar), "blakberrie" (NE), "baslerd," "bolletrie," 23-IX-1916, *Stahel & Gonggryp* 3570 (U).

FRENCH GUIANA: St. Jean, Concession Bonnet, 24-V-1914, *Benoist* 1239 (P). Acarouany, 1858, *Sagot* s.n. (P). Route de l'Acarouany au km. 5, coté gauche de la route, fleurs blanchâtres en grappes formant corymbe axillaire en pointe des rameaux, "bonga-bitá" (Paramaka), 5-XI-1956, *BAFOG* 7587 (U). Km 4 coté droit et à 20 m. de la route, fruit vert, léger-ovales ressemblant a des petites olives; inflorescences à la pointe des rameaux, "bonga-bitá," 29-IX-1954, *BAFOG* 228M (U). Cayenne, arbe, "bois rouge," 14-XII-1955, *BAFOG* "P. Benti" 1083 (U). Cayenne, *Martin* s.n. (BM, P). Cayenne, 1857, *Sagot* s.n. (P). "Guyane française," without locality, *Melinon* 1863 or 1864 (A, GH, MO, NY, P, US), *Melinon* 48 (P); *Melinon* 377 (P, K). *Herb. Exp. Col.* (P), ex *Herb. Richard* (P), ex *Herb. Cosson* (P); *Le Prieur* 1838, 1840 (P, K).

BRAZIL: AMAZONAS: Manaos, Cachoeirinha circa ripas paludosas Igarapé do Crespo, arbuscula floribus albis, *Ducke* 23424 (US). Rio Vaupes, Taraquá, caatinga proxima a serra, arvore 15-20 m., flor branca, frutos comestiveis, "umiri," 10-XI-1947, *Pires* 989 (IAN, NY, P, US). Rio Curicuriary, afluente do Rio Negro, silva ad ripas altas cataractae Cajú; arbor mediocris floribus albis, cortice odorato, "umiry," 29-II-1936, *Ducke* 30128 (MO, F, K, US, U, P). AMAPÁ: Oiapoque, campo de aviação campina arvore pequena, 3-X-1949, *Black* 49-8313 (IAN). Oiapoque, caño Inocencia, arvore, 4-X-1949, *Black* 49-8369 (IAN). Oyapock Airfield, infrequent, secondary forest, tree 5 m. tall, 7-XII-1954, *Cowan* 38700 (NY). Estrada Macapá-Clevelandia, km. 130, arvore flor branca, 27-VIII-1955, *Black* 55-18577 (IAN). RIO BRANCO: Caminho de Samauma a campo de aviação de Mucajá, kms. 14-15 da estrada Boa Vista-Caracá, arvore pequena, flor branca, 25-VIII-1951, *Black & Magalhães* 51-12954 (IAN, P). Rio Branco, entre as Fazendas Bom Intento e Capela, flor branca, 31-VIII-1951, *Black* 51-13231 (IAN). PARÁ: Belém, Lago da Agua Preta, 29-X-1914, *Ducke* 15514, 15515 (MG). Pará, *Moss* 13 (US); *Moss* 57 (US, NY). Santa Isabel

(Estação Ferr. Bragança), VI-1908, *Museu Goeldi* 9419 (MG). Igarapé Gameleirinha, campos gerais, região do Araguaia, arvore 7 m., flor branca, 17-VI-1953, *Fróes* 29854 (IAN). Rio Maicurú, estrada Caá-ussú a Serra de Luna, campina arenosa, municipio de Monte Alegre, arvore de 5 m., flor esbranquiçada, 9-III-1953, *Fróes & Filho* 29486 (IAN, US). Tefé, mata virgem, arvore 30 m., flor branca, madeira bonita, vermelha carregada (amago), flor cheirosa, "pau mirim," 25-VIII-1947, *Black* 47-1276 (IAN, NY, U, US, VEN). Marajó, Jutuba, matta de marjem, arvore alta, 21-VII-1902, *Huber* 2785 (BM, MG). Without data, *Schultes* 9431a, 9435 (IAN).

1a(2). *Humiria balsamifera* var. *balsamifera* fma. *attenuata* Cuatr., fma. nov
 FIGURES 21,b-c,g; 22,d; 23,p

A forma *balsamifera* typica differt folia basi late attenuata (nec auriculata) sessilia.

Type in the U.S. National Herbarium, No. 2171627, collected on quartzite rocks of falls at Raudal Yayacopi (La Playa), 800 ft. altitude, Río Apaporis, Amazonas-Vaupés, Colombia, February 18, 1952, by Richard Evans Schultes and Isidoro Cabrera, No. 15511.

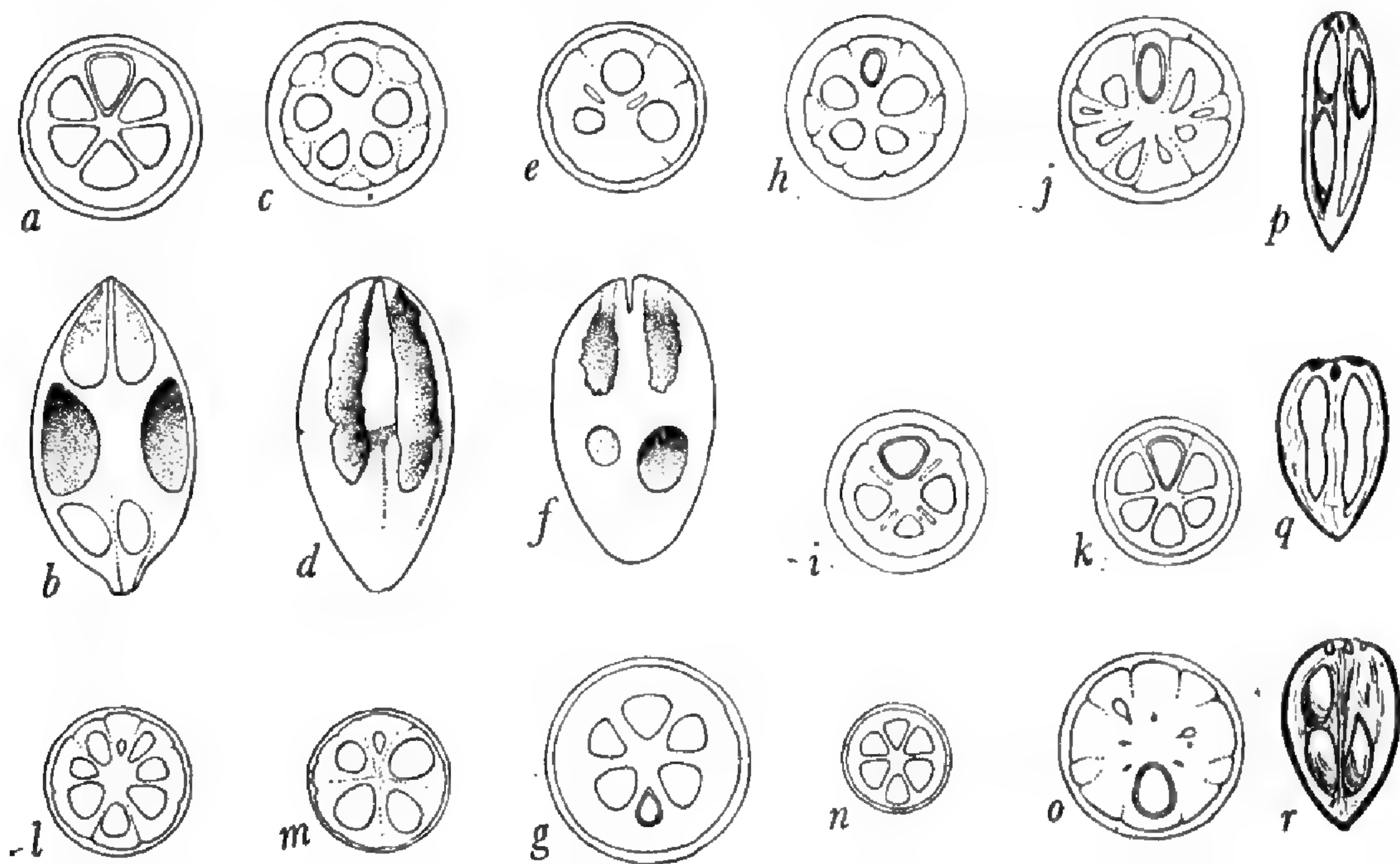


FIGURE 23.—*Humiria* fruit: a-d, *H. balsamifera* var. *floribunda*: a, transection (*Maguire & Maguire* 35040); b, longitudinal section; c, transection (*Black* 47-1756); d, longitudinal section. e-g, *H. balsamifera* var. *coriacea*: e, transection (*Maguire et al.* 30018); f, longitudinal section; g, transection (*Maguire & Politi* 27695); j-k, *H. balsamifera* var. *subsessilis*: j, transection (*Williams* 13868); k, transection (*Cowan & Wurdack* 31472). l-m, *H. balsamifera* var. *guianensis*: l, transection (*Hitchcock* 16938); m, transection (*Maguire & Politi* 28828). n, *H. balsamifera* var. *stenocarpa* (*Maguire & Maguire* 40105), transection. o, q, r, *H. crassifolia* (*Maguire & Fanshawe* 23233): o, transection; q, shape of endocarp with oblong and pitched valves corresponding to superposed cavities; r, longitudinal section of the same endocarp to show two superposed cavities and ovules at one side and one ovule in its cavity with sterile upper cavity at the other side. p, *H. balsamifera* fma. *attenuata*, longitudinal section of endocarp showing two superposed cavities and ovules from one carpel and a single ovule developed in another carpel (*Fróes* 22738).

This is just a form of the typical *H. balsamifera* with attenuate leaves at base. It is found in somewhat dryer parts than the typical form, in sandy or sandstone places, in savanna remnant forests or thickets, etc.; the morphologic difference probably depends very much on local ecological conditions. It is spread from the four Guianas through the Amazon basin to the Huallaga River in Peru and to Belém (Pará) and Goiás in Brazil.

COLOMBIA: VAUPÉS: Río Apaporis, raudal Yayacopí (La Playa), quartzite base, alt. 800 ft., small tree, 18-II-1952, *Schultes & Cabrera* 15511 (US, holotype); on sand, small black edible fruit, "wa-too-moo-ko" (Yukuna), 18-VIII-1952, *Schultes & Cabrera* 16893 (US).

VENEZUELA: BOLÍVAR: Región de los ríos Icaború, Hacha, 450-850 m., sabana, árbol aislado en la sabana, corteza rayada, hoja coriácea, 24-XII-1955, *Bernardi* 2601 (NY).

BRITISH GUIANA: Mazaruni Station, mixed forest, tree 90 ft. high, 17 in. diam., bark dark brown, fissured; wood hard, heartwood red, "tawasansu," 12-V-1933, *Tutin* 83 (U, BM, US). Basin of Rupununi River, Isherton, "umir" (Wapisiana), *A. C. Smith* 2423 (A, F, MO, NY, Y, US, S). Atkinson Field, at the east border, tow tree in open dry bush, flowers white, odoriferous, 2-V-1954, *Irwin* 246 (US). Lucky Spot, sandbank, tree, flowers white, X-1924, *Persaud* 191 (F, K, NY). Massaroonie v. Essequibo, "bastard bully-tree," "towraneroo," *Appun* 37 (K).

SURINAM: Prope Patrick-Savanna, 5-V-1910, *Boschwezen* "Indig." 177 (U). Boschreserve, Sectie O, 1-XI-1920 *Boschwezen* 4770 (U); *Boschwezen* 5850 (U, IAN). Zanderij 1-X-1942, "tawalāenra," "tawalāngro" (Arow), "meri" (Ka), "basrabolletrie," *Stahel* 90 (A, IAN, NY, U, Y). Vicinity Arawak Village of Mata, tree, 18-X-1944, *Maguire & Stahel* 24957 (NY, U). Boven Sipaliwini, kamp IV, groote savanne, 2 NB, 56 WL, 23-X-1935, *Rombouto* 228 (U).

FRENCH GUIANA: "Guyane," *Poiteau* s.n. (K).

BRAZIL: RIO BRANCO: Uferwald bei Boa Vista, Strauch 3-8 m., X-1908, *Ule* 7625 (US, K, UC). Igarape Caraná, arvore em campo seco, flor branca, 20-VIII-1951, *Black* 51-12776 (IAN). AMAZONAS: Rio Demeni, affluente do Rio Negro, Posto Indigena Genipapo, caatinga, arvore 15 m., 12-X-1952, *Fróes* 28895 (IAN, US). Rio Negro, Preto Campina, tree 25 ft., whitish flowers, rather grassy country, sandy soil, 5-XI-1957, *Fróes* 22738 (IAN, NY, US, VEN). Manaus, shrubby tree, 20 ft., *Tate* 50 (NY). PARÁ: "Prov. Para," *Martius* s.n. (M). Belém, near Catu, 8 km. northeast of Inst. Agr. do Norte, tree 20 m., fruits olive-colored, edible, a local drugstore sells a syrup made from bark for relief from constipation, "mirim," 15-IX-1942, *Barbosa da Silva* 73 (IAN, US). Vigia, Campina do Palha, arvore pequena, fruto verde, 29-IX-1948, *Black* 48-3249 (IAN, P); solo arenoso, arvore 12 m., flor branca muito cheirosa, 10-VI-1952, *Fróes* 28454 (IAN, US); bordos e ilhas da matta, arvore pequeno, flores alvo-cremes, "umiri," 29-IV-1953, *Lima* 53-1273 (IAN). Obidos, beira do lago, flor branca, 12-VII-1905, *Ducke* 7213 (BM, MG). Rio Guamá, acima de Ourón, porto do Posto Indigena Tombé, arvore grande, flor branca, matta de várzea, VI-53, *Pires & Silva* 4629 (NY), 4624 (IAN). Goiás: Carolina, arvore de terras frescas, Branca, "meirin" (pan-meirim), 11-VIII-1955, *Macedo* 4034 (IAN, US).

PERU: LORETO: Miahuyaco, near Iquitos 100 m., forest, tree 18 m. high, flowers white, V-1930, *Klug* 1315 (F, US). Balsapuerto, 200 m., tree 4 m., flowers white, I-1933, *Klug* 2846 (A, BM, F, GH, MO, NY, S, US). Balsapuerto,

lower Rio Huallaga basin, 150–350 m., dense forest, 28–30–VIII–1929, *Killip & Smith* 28681 (F, NY, US).

1b. *Humiria balsamifera* var. *floribunda* (Martius) Cuatr., comb. nov.

FIGURES 21,*d–f*; 23,*a–d*; 24,*c*; PLATE 4

Humirium floribundum Mart. Nov. Gen. Sp. Pl. 2:143, pl. 199. 1827.—

Benth. in Hook. Journ. Bot. Kew Miscel. 5:100. 1853.

Humirium multiflorum Pritz., Ic. Ind. 560. 1866.

Humiria floribunda Mart. Urb. in Mart. Fl. Bras. 12(2):437. 1877.—Ducke,

Arch. Jard. Bot. Rio Janeiro 3:176. 1922.—Arch. Inst. Biol. Veget.

Rio Janeiro 4:25. 1937.

Humirium ellipticum Klotsch ex Urb., *ibid.*, as synonym.

Type: *Martius*, Brazil, Pará, Xingú (M).

Leaves attenuate toward cuneate base, petiolate or subsessile, elliptic, obovate-elliptic or somewhat oblong; slightly attenuate and obtuse, often emarginate, sometimes rounded or truncate at apex; glabrous but rarely with pubescent midrib beneath; margin usually minutely crenate, glandular-punctuate beneath or eglandular; 4–12 cm. long, 2–6 cm. broad. The young branchlets generally glabrous or sometimes puberulous, angulate or subterete, rarely narrowly winged.

The binomial *Humirium multiflorum* is the result of an erroneous quotation by Pritzel, which has never been validly published. Spach (1846) described two species with a French title followed by the corresponding Latin binomial; one species is “*Humirium de Guiane*” (= *Humirium balsamiferum* Aubl.), and the other is “*Humirium multiflore*” (= *Humirium floribundum* Mart.). The adjective “*multiflore*” is here merely the French translation of *H. floribundum*. Pritzel erroneously latinized this adjective to a specific name.

The variety *floribunda* is widely spread throughout the Amazon Basin, from Venezuela, Guianas, and Surinam to the southern States of Brazil in Rio de Janeiro. It can be found in the rain forests on uninundatable ground, as well as in open places in savannas and campos. According to Ducke, it is common in the State of Pará on white sandy soils containing some humus and is the typical tree of the “campinas”; it varies from a small shrub scrambling on the stony campos of Ariramba to a large tree of 30 m. height in the forests near Belém. Ducke mentions intermediary forms between var. *floribunda* and *balsamifera* between Belém and Bragança. According to Ducke, *floribunda* produces the “umiry balsam” which smells like the Peruvian balsam. “This ‘umiry balsam’ is only produced by the more or less sick old trunks of the forest. I have never seen this balsam in trees located in open places; it seems to be due to an illness of the tree probably caused by bacteria. The drupes of this variety are edible, sweet, and agreeable, especially those from

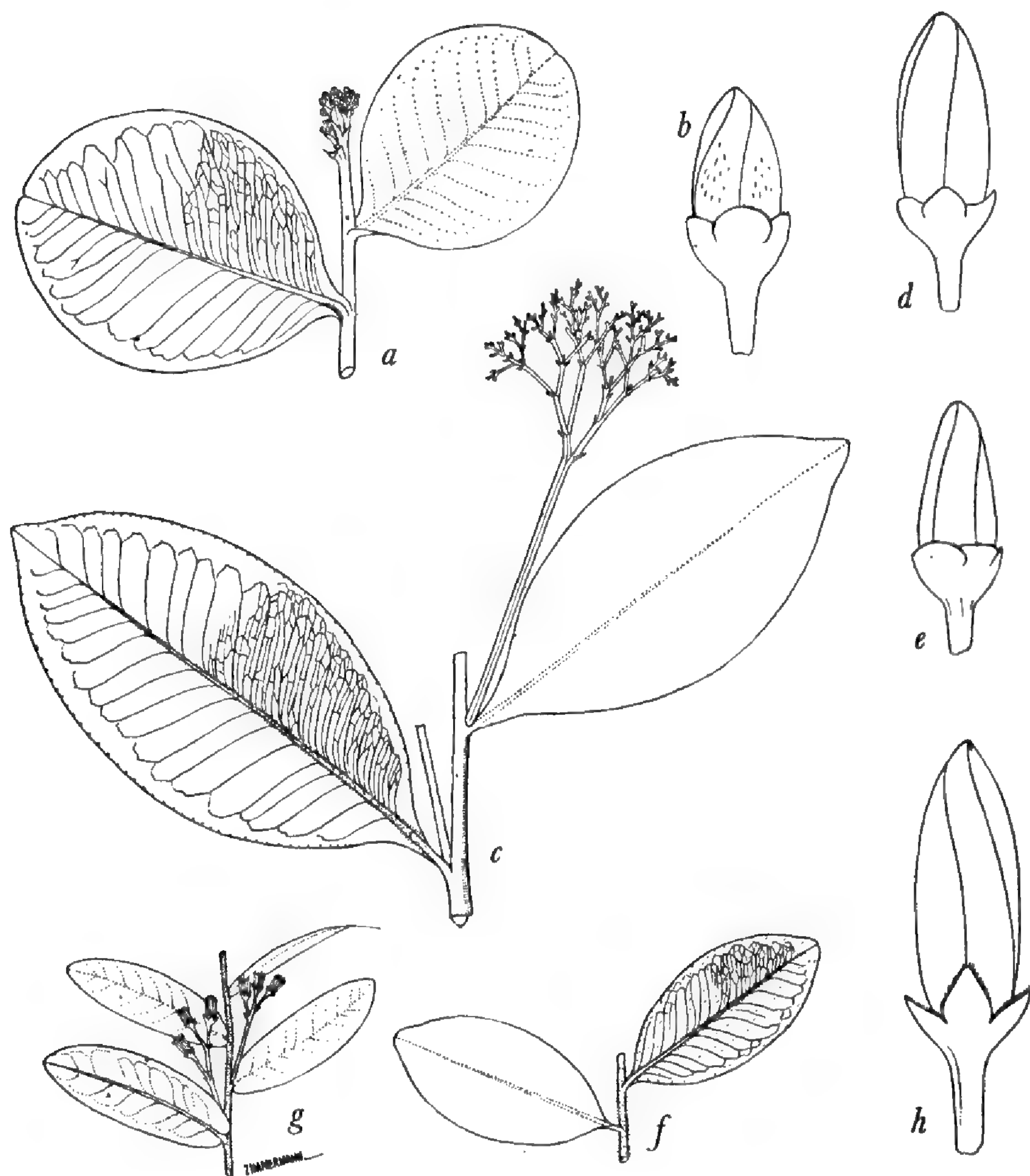


FIGURE 24.—a-f, *Humiria balsamifera*: a, var. *guaiquinimana*, $\times \frac{1}{2}$ (Cardona 1112); b, var. *coriacea*, bud, $\times 5$ (Maguire & Fanshawe 23295); c, var. *floribunda*, $\times \frac{1}{2}$ (Riedel s.n.). d, var. *laurina*, bud, $\times 5$ (Krukoff 1483); e, var. *parvifolia*, bud, $\times 5$ (type of "*H. montanum*," St. Hilaire); f, var. *pilosa*, leaf, $\times \frac{1}{2}$ (Steyermark 60289); g, *Humiria fruticosa*, $\times \frac{2}{3}$ (Maguire et al. 36580); h, *Humiria fruticosa*, bud, $\times 5$ (Maguire et al. 36580).

the trees of the campos and campinas, whereas I have found those of the rain forest to be insipid."

VENEZUELA: AMAZONAS: Cerro Sipapo, forest near Base Camp, alt. 125 m., small tree with greenish white flowers, 28-XII-1948, Maguire & Politi 27974 (NY, US). Serrania Yutaje, Rio Manapiare, Base Camp, alt. 200 m., occasional at savanna edge 1 km. east of Base, shrub or small tree, 4-10 m. tall, fruit green, 29-I-1953, Maguire & Maguire 35040 (NY, US). Cerro Moriche, occasionally in sabanita at northwest base of mountain, alt. 150 m., tree 3 m., fruit green, 17-I-1951, Maguire, Cowan, & Wurdack 30987 (NY, US).

BRITISH GUIANA: Along the Berbice-Rupununi Cattle Trail, Berbice or Demerara County, 29-V-1919, *Abraham* 152 (NY).

SURINAM: Jodensavanne-Mapane Kreek area (Suriname R.); op droge zandsavanne acter Suhoza; struik, bloem wit, 10-VII-1953, *Lindeman* 4201 (U); op droge zandsavanne aaen Blakawatra, struik, "blakaberie" (Sur.), 17-XII-1954, *Lindeman* 6862 (U). Via secta ab Moengo tapoe ad Grote Zwiebelzwamp; in ritsbos bij km. 14.9; boom 17 m. 18 cm. dik, "blakaberie" (Sur.), 25-X-1948, *Lanjouw & Lindeman* 968 (U).

FRENCH GUIANA: Cayenne, west, frequent small tree in islands of trees in white sand savannas, 26-X-1954, *Cowan & Maguire* 38034 (NY). "Guiana fr.," *Leblond* 441, 402 (P). *Donant Herb.* 1686, without locality (P).

BRAZIL: RIO BRANCO: Serra da Malacacheta, "umiry," *Kuhlmann* 3509 (US). Uferwald bei Boa Vista, Bl. weisslich, Strauch 3-8 m., X-1908, *Ule* 7625 (MG). AMAZONAS: Manaus, margen do Igarapé do Buião; terra firme, capoeira, arvore de 6 m. alt., flor branca, 31-VIII-1955, *INPA* 1773 (MG, US). Manaus, prope Cachoeira alta do Tarumá, silva non inundabili loco humido; arbor mediocris floribus albis, 25-IV-1932, *Ducke* 87 (A, Y). Manaus, Colonia João Alfredo, arvore de flor ligeiramente rosea, 17-VIII-1954, *INPA* 86 (MG, US). Manaus, Igarapé do Parque 10, terra firme; arvore de 10 m., flor branca, 25-V-1955, *INPA* 1056 (MG, US). Manaus, Rio Negro, IX-1948, *Schultes & Lopez* 10339. Manaus, arvore, "humiry," 15-II-1945, *Fróes* 20480 (IAN, US). Municipality of Manaus, Rio Negro basin, along road to Aleixo, campinarana, VIII-IX-1936, "mirim," tree 40 ft., trunk 4 in. diameter, flowers white, *Krukoff* 7928 (A, NY, BM, S, U); "mirim," tree 45 ft., 5 in. diameter, flowers white, *Krukoff* 7926 (A, BM, F, MO, NY, S, U). Campinarana, Rejas do Alto Ariramba, 20-XII-1906, *Ducke* 8029 (BM, MG). Manaus, circa Cachoeira da Mundú, silva non inundabili; arbor parva, flos albis, "umiry," 2-IX-1942, *Ducke* 541 (IAN, MG, NY, S, US). Rio Negro, Aiary-Pirá, Rio Aiary, caatinga arenosa, arvore, 5-XI-1945, *Fróes* 21346 (IAN, NY, US). Rio Negro, prope Barra, 1851, *Spruce* 1499 (NY, GH, BM, K, M, US, S, P). MARANHÃO: Cururupú, *Lisboa* 4099 (US). Grajaú, 13-VIII-1909, *Lisboa* 2327 (US). Ilha de São Luiz; reservatorio Socaven; terra firme, baixa, floresta alta; arvore de 5 m., flor branca, 15-I-1951, *Fróes* 26812 (IAN). Ilha de São Luiz, São Simão, campinarana, tree 60 ft. 9 in., "umiry," 1940, *Fróes* 11813 (NY). Alcântara; taboleiros descampados de beira mar, 28-IX-1903, *Ducke* 440 (BM, MG). Bords du Rio Tocantins, VIII-IX-1844, *Weddell* 2361 (P). AMAPÁ: Rio Araguari, campos gerais, arvore 7 m., flor branca, 22-VII-1951, *Fróes & Black* 27572 (IAN). PARÁ: Santarém, January, *Spruce* 928 (K, P). In vicinibus Santarém, VI-1850, *Spruce* s.n. (P, BM, GH). Perto da Casa Santa Izabel, municipio de Santarém, campo coberto, arvore pequena, "umiri," 28-X-1950, *Black & Ledoux* 50-10371 (IAN). Caripi, VIII-1849, *Spruce* 928, 181 ? (NY), 181 (M). Caripi, on the beach, low round-topped tree with roughest sweet-scented bark, flowers white, "umiri," VIII-1849, *Spruce* 164 (K, P). Rio Arapius, 6-VI-1952, *Pires & Silva* 4192 (IAN, NY). In ripis amnis Parae et St. Antonii *Herb. Richard* (P). Gurupá, campina do Igarapé Jucupí; arvore mediana, flor branca, 18-VIII-1954, *Pires & Silva* 4702 (IAN, US). Conceição do Araquáia; terreno arenoso, úmido a beira dos campos de transição para a mata dos carrascos; arvore de 10 m., 3-VII-1953, *Fróes* 30093 (IAN, US). Rio Jamaracarú, perto do barracão; arbusto reptante; flor branca perfumada, 26-V-1957, *Black, Egler, et al.* 57-19590 (IAN, US). Obidos, Rio Jaramacurú, sandy and over-flowed field, plant of 50 cm., corolla white, 27-V-1957, *Egler* 261 (MG, US). Belterra, beira do R. Tapajós igapó; arbustivo espalhado, flor branca, fruto verde, "umiri," 24-X-1947, *Black* 47-1756 (IAN, NY, US, U, VEN). "Iter Brasil. Sept. habitat in ripa ad flumen Xingú ostia

locis arenosis, Provinciae Paraënsis, Mart. Observ. 2692, *Myrodendron petiolatum* Mart. tab. 195," *Martius* s.n. (M, holotype of *Humirium floribundum*). "Brasilia Prov. Pará, Umiri Paraënsibus Martius Observ. 2692," *Martius* s.n. (M, isotype of *Humirium floribundum*). CEARA: Fortaleza, Huber 96 (BM, US). Bemfica, 10-IX-1907, Huber 96 (MG). "Ceará," Allemão & Cysneiros 255 (US). BAHIA: Salzman s.n., no locality (P). RIO DE JANEIRO: Restinga de Cabo Frio; arbrisseau, fleur blanc jaunâtre, 20-VI-1877, Glaziou 10437 (P). Inter Rio de Janeiro et Campos, Sellow 171 (K). Environs de Rio de Janeiro, Weddell 526 (P). Without locality Sellow s.n. (M, NY); Riedel s.n. (P). Versus Colares, Poeppig s.n. (P). "Amerique Meridionale-Poeppig, 1868 No. 34," Poeppig 3011 (P). Prov. of Alagoas, Maceio, IV-1838, Gardner 1263 (BM). Without locality, Poeppig 81 (BM).

1c. *Humiria balsamifera* var. *subsessilis* (Urb.) Cuatr., comb. nov.

FIGURES 21,k-n; 22,e; 23,j-k

Humiria floribunda var. *subsessilis* Urb. in Mart. Fl. Bras. 12(2):439. 1877.

Humirium subsessile Spruce ex Urb. in Mart., ibid., as synonym.

Type: Spruce 2454, Brazil, Vaupés.

Leaves subcoriaceous, rigidulous, sublanceolate-elliptic or rhomboid-elliptic, slightly attenuate, obtuse, subrotundate, rarely amplexant at base, attenuate and obtusely acuminate at apex, sometimes minutely emarginate, the margin crenulate and glandular-punctate beneath; the midrib densely hirtellous, puberulous or glabrous; 3.5-10 cm. long, 1.5-4 cm. broad. Branchlets wingless, hirtellous, puberulous, or also glabrous. Pedicels and sepals hirtellous or glabrous. Petals glabrous or puberulous. Drupe ellipsoid-ovoid, 11-12 \times 7.5-8.5 mm.; the endocarp verruculose, 9-11 \times 5-7 mm., acute at apex.

The type has the branchlets, nerves of the leaves beneath, pedicels, and sepals hirtellous-pubescent; but few of the other collections (Spruce 2454, Pires 1029) have these features; most of the specimens lack the indument on pedicels and sepals, whereas in others it becomes scarce on branchlets and leaves and passes gradually to the glabrous forms. But the elongate-elliptic, sublanceolate leaves, which are narrowed toward the obtusely subacuminate apex, are a typical feature that characterizes a consistent variety spread from the Vaupés River to the Guiana plateaus. It does not have obovate, spatulate, or broadly obtuse leaves (not attenuate at apex in adult stage) as do varieties *balsamifera* and *floribunda*.

The range of *subsessilis* extends from the Brazilian and Colombian Vaupés to the Negro and Orinoco Rivers and the southern savannas of Venezuela. Undoubtedly the *Humiria* population of the west coast of Colombia refers to the same variety.

COLOMBIA: VAUPÉS: Río Piraparaná, tributary of Apaporis, Caño Timiña, large bush, flowers white, "ta-ta-wee-tee-go" (Barasana), 6-IX-1952, Schultes & Cabrera 17231 (US). Río Cubiyú, cerro Cañendá, sabanas 15 millas arriba de la bocana, alt. 800-900 ft., small tree, bushy, 20 ft., flowers white, 10-XI-1952,

Schultes & Cabrera 18319, 18371 (US). Río Cubiyú, alt. 350 m., 9-10-X-1952, *Humbert & Schultes* 27364 (US). Río Negro, vicinity of Piedra del Cocui, bush, caatinga, 27-XII-1947, *Schultes & López* 9510 (IAN, NY). Río Negro, San Felipe, alt. 200 m., 13-25-XI-1952, *Humbert* 27422 (P). Región de San Felipe a orillas del Río Guainía, 250 m. alt., árbol 4 m., frutos verdes, 21-XI-1948, *Araque & Barkley* 18 Va021 (US). Valle, Costa del Pacífico, Bahía de Buenaventura, Quebrada de Aguadulce 0-10 m. alt.; árbol, hoja coriácea, flexible, verde oscura semibrillante haz, claro envés; perianto verde pálido, blanquecino, "oloroso," 11-XI-1945, *Cuatrecasas* 19727 (COL, G, U, F).

VENEZUELA: AMAZONAS: Region of San Fernando de Atabapo, Río Orinoco, frequent on laja on left bank of Caño Cupueni opposite mouth of Río Atabapo, rounded dark green tree, 15 m. tall, flowers white, 12-XI-1953, *Maguire, Wurdack, & Bunting* 36210 (US, NY). Between Sabana Grande and southeast base of Cerro Duida, alt. 200 m., 23-VIII-1944, *Steyermark* 57880 (US, F). Río Orinoco, Río Cunucunuma, edge of Culebra savanna, north base of Cerro Duida, alt. 200 m., much branched tree, 10 m., flowers greenish white, 27-XI-1950, *Maguire, Cowan, & Wurdack* 29769 (US, NY); 13-XI-1950, *Maguire, Cowan, & Wurdack*, 29416A (US, NY). Río Ventuari, savanna on Caño Arisa at west base of mountain, alt. 200 m., locally frequent, tree 6 m., fruit green, 16-II-1951, *Cowan & Wurdack* 31502 (US, NY); tree to 10 m., fruit purple-black, edible, 15-II-1951, *Cowan & Wurdack* 31472 (US, NY). Esmeralda, alt. 325 ft., tree savannas, flowers white, *Tate* 330 part (first sheet) (NY); *Tate* 331 (US, NY). Yavita, 280 m. alt. en terreno rocoso y abierto; árbol 5 m. o más con copa casi plana, tronco redondo, corto, 10 cm. diám., madera clara; fruto monospermo, azulejo o casi negro de pulpa algo dulce y comible, "niña," 22-I-1942, *Llewelyn Williams* 13868 (US). BOLIVAR: Soropán-tepuí, wooded ridge, between quebrada and waterfall, alt. 1,656-1,980 m., small tree 25 ft.; leaves subcoriaceous, dark green above and shining, dull green below; "coporik-warei-yek," *Steyermark* 60192 (NY).

BRAZIL: AMAZONAS: Vaupés, Panure, caatinga; arvore pequena, flor branca, 15-XI-1947, *Pires* 1029 (IAN, VEN). Panure, IX-1952 to I-1953, *Spruce* 2457 (GH, BM, NY, MG, P). Prope Panure, IX and XII-1952, *Spruce* 2454 (isotype of *H. floribunda* var. *subsessilis*, BM, F, GH, NY, P, S). Ipanoro, Rio Vaupés, between Ipanoré and confluence with Río Negro, small tree, flowers green-white, 14-15-XI-1947, *Schultes & Pires* 9103A (US, IAN). Rio Xiborem, weiss, am Ufer, 15 m., 30-VIII-1928, *Luetzelburg* 24014 (M).

1d. *Humiria balsamifera* var. *guianensis* (Benth) Cuatr., comb.nov.

FIGURES 21,*h-i*; 22,*g-h*; 23,*l-m*; PLATE 5

Humirium guianense Benth. in Hook.London Journ.Bot.2:374. 1843.—
Hook. Journ. Bot. Kew Miscel.5:100. 1853.

Humirium surinamense Miquel, Stirp.Surinam 86, pl. 24. 1850.

Humiria floribunda var. *guianensis* (Benth.) Urb. in Mart. Fl.Bras.12(2):
439. 1877.

Myrodendron petiolatum Mart. ex Urb., ibid., as synonym.

Humiria Cassiquiari Sussenguth & Bergdolt, Repert. Sp. Nov. Fedde 39:16.
1935.

Type: *Schomburgk* 270, British Guiana.

Leaves coriaceous or subcoriaceous, broadly obovate or suborbicular, abruptly contrated into winged petiole, rounded, emarginate or very obtuse at apex; the midrib generally hirtellous-pubescent beneath, sometimes glabrous, the margin more or less conspicuously crenulate,

rarely entire, usually glandulose-punctate beneath; blades 3–12 cm. long, 2.5–6 cm. broad. Petiole 0.5–2.5 cm. long. The young branchlets pubescent or puberulous, rarely glabrous.

The variety *guianensis* may be a medium-size tree, but it is most commonly a small tree or shrub producing small blackish or blue-black berries that are more or less sweet and flavorful. This variety is very much spread throughout Surinam, British Guiana, the Amazon territory of Venezuela, the Río Negro-Guainía region of Columbia and Brazil, and Rio Branco in Brazil, with small incursions into the Pará region. It is found in thickets and in marginal forests, and is also isolated in campos, campinas, caatingas, and savannas. Although its typical form is very characteristic, intermediate forms transitional to variety *floribunda* are very often found.

H. cassiquiari Suss. & Bergd. cannot be separated from variety *guianensis*. The type, *Lutzelburg* 22627, does not differ in any way from other abundant specimens seen of *guianensis*, which often have a retuse or emarginate apex with a mucro in the bottom of the depression. This natural notch is often widened by some exterior cause, such as insect eating or some kind of burning. The mucro, with a glandular appearance at the tip, is seen only in young leaves, for it usually breaks off. The petals in *H. balsamifera* sensu lato sometimes end in a small glandular or pseudoglandular tip. This is more or less apparent or inconspicuous and cannot be used as a taxonomic character. The inflorescences of the typical specimens of *H. cassiquiari* are very young and the few buds present are too underdeveloped to typify the floral characters of a species. In 1 of these buds, 18 stamens could be counted, but in some normal specimens of *H. balsamifera* sensu amplo, I also have observed very rare flowers with some reductions in the number of stamens.

COLOMBIA: VAUPÉS: Raudal Guacamayo en el Río Inírida, margen izquierda, 180 m. alt., arbolito 4–5 m., frutos color verde, 4–II–1953, *Ferdández* 2148 (COL, US). Río Negro, at confluence of Rivers Guainía and Casiquiare, Caño Ducurupo, Igarapé Rana, tree, *Schultes & López* 9363 (F, IAN). Río Negro a San Felipe, alt. 200 m., 13–25–XI–1952, *Humbert* 27440 (US). Río Atabapo, bushy sprawling tree 1–5 m., flowers greenish white, frequent in savanna 1 km. west of Cacagual, alt. 130 m., 19–XI–1953, *Maguire, Wurdack, & Bunting* 36295 (NY, US).

VENEZUELA: AMAZONAS: In sylvis humilioribus fluminis Guainia, XI–1954, arbor ramosa 15–20 ft., *Spruce* s.n. (K). Río Guainía, frequent in sabanita 1 km. west of La Ceiba, Caño San Miguel, 2 km. above Limoncito, shrubby tree 2–5 m. in bud, *Maguire, Wurdack, & Keith* 41917 (NY, US). Río Guainía, riverine forest just south of Maroa, tree, flowers white, fruit green, 28–XI–1953, *Maguire, Wurdack, & Bunting* 36456 (NY, US). Orinoco, Cerro Yapacana, shrub or tree to 5 m., flowers white, locally frequent in savanna No. 3, northwest base of mountain, alt. 125 m., 1–I–1951, *Maguire, Cowan, & Wurdack* 30543 (NY, US); occa-

sionally in savanna No. 1, northwest base of mountain, alt. 125 m., 7-I-1951, *Maguire, Cowan, & Wurdack* 30791 (US, VEN). Cerro Sipapo (Paraque), open shrub savanna on white sand, 3 km. southwest of Base camp, alt. 200 m., 8-II-1949, *Maguire & Politi* 28828 (NY, US). Yavita, terreno abierto, arenoso, 128 m. alt., árbol pequeño o arbusto 2 m., flores amarillo pálidas, fruto azulejo o casi negro, jugoso; corteza áspera, rojo oscura, madera rosada, 22-I-1942, *Llewelyn Williams* 13903 (US). "Pacimoni, Fl. Febr. 1854," "Ad flumina Casiquiari Vasiva et Pacimoni coll. R. Spruce, 1853-54," *Spruce* 3409 (P,K,S). I savanna prope Blaauwe Berg, missit de Vacibe 1849, collector ? (S). Cassiquiare, Ufer, Laja de Caraça, orange, 4 m. 5-X-1928, *Luetzelburg* 22627 (M, holotype of *Humiria cassiquiari*). Cassiquiare, Buenos Aires, Uferwald, gelb, 6 m., 6-X-1928, *Luetzelburg* 22561 (M, paratype). Laja de Caraça, Ufer, weiss, 9-X-1928, *Luetzelburg* 22575 (M, paratype).

BRITISH GUIANA: Basin of Essequibo River, Kurupukari, slender tree 3 m., petals and filaments white, on burned forest land, 3-X-1937, *A. C. Smith* 2176 (A, F, NY, S, U, US). Upper Mazaruni River, IX-X-1922, *De La Cruz* 2210, 2227 (F, GH, MO, NY, US); *De La Cruz* 2202 (MO, NY). Demerara River, Malali, 30-X-5-XI-1922, *De La Cruz* 2644 (MO); *De La Cruz* 2645 (F, GH, MO, NY, UC, US). Demerara River, Mahaica-Mahaicany, "muri," fruit edible, *Forest Dept. (Anderson)* 559 (K). Demerara, savanna plant, 21-II-1910, "muri," *Forest Dept. (Anderson)* 506 (K). Lungo il fiume Demerara, "muri bush" nella regione delle Canister Fall (Camo IV), 5-XI-1931, "muri," *Beccari* s.n. (K). Demerara, V-1889, *Jenman* 4883 (BM, K). Waranama Ranch, Wirumi-Ituni savanna, Nkuri white sand area; a dominant bush in Nkuri-association; glaucous leaves; small, inconspicuous flowers; fruits green, black when ripe, edible; *Martyn* 136 (NY). Kaieteur Savanna, Potaro River, IX-X-1881, tree 15 ft., *Jenman* 1281 (K). Kaieteur Plateau, occasionally shrubby, procumbent, 1 m. high, clump, flowers white, buds light green, 14-V-1944, *Maguire & Fanshawe* 23450 (NY, U, US). Rupununi River, Qumatta, X-1889, *Jenman* 5561 (NY), *Jenman* 5562 (NY, US). Rupununi River, near Apoteri, alt. 300 ft., small tree with flat spreading crown up to 20 ft., in savanna caused by fire on white sand soil liable to inundation, *Forest Department* 2055 (K). Corentyne River, sand ridge woods, tree 20 ft. or more, *Jenman* 299 (P). Savannas east of Itumi, 35 miles south of Makenzie, frequent in margin of forest "islands," tree, flowers white, fruit green, 17-I-1955, *Cowan* 39266 (NY); semi prostrate tree, *Cowan* 39263 (NY, US). East Coast Water Conservancy, southeast of Georgetown, sand reef at head of Hoorubia Creek, sandy scrub, 26-XI-1919, *Hitchcock* 16938 (GH, NY, S, US). "British Guiana," *Schomburgk* 270 (P, NY, US, isotypes), photo F.M. 35176 at P. "British Guiana, Oct. 19," shrub 5-12 ft., fruits greenish white, collector ? (P).

SURINAM: Boschreserve, Sectie 0, 3-VIII-1920, witte bloeme, shrub of savanna, *Pulle* 150 (U); 20-XII-1906, *Boschwezen* 36a (U); 21-II-1918, *Boschwezen* 3646 (IAN, U); Boomnummer 842, 23-IV-1917, *Boschwezen* 2816 (U); 20-XII-1916, *Boschwezen* 2599 (U); 8-VIII-1918, *Boschwezen* 3947 (U); 2-VIII-1917, *Boschwezen* 3040 (U); Zanderij I, 26-IV-1915, *Boschwezen* 531 (U). Zanderij I, 10-XI-1921, *Boschwezen* 5486 (U). Zanderij I savanna a, struik 1½ m., vrucht groen, onrijp, "blakaberie," 10-III-1949, *Lanjouw & Lindeman* 3259 (U). Zanderij I, savanna, flowers white, shrub, 22-VII-1923, *Lanjouw* 195 (U, US). Zanderij I, savanna bij vliegveld, struik, bloem groenachtig-wit, 9-IX-1948, *Lindeman* 258 (U). Zanderij I, savanna voor vliegveld, struik bloem wit, 9-IX-1948, "tauraroe" (Arow.), *Lanjouw & Lindeman* 267, 268 (U). Zanderij

I, savanna, sand, flowers white, fruit green, shrub (may become a large tree), "blakkaberie," 30-VII-1933, *Lanjouw* 334 (U). Zanderij I, indianenkamp, "tawararoe" (Arow.), "meri" (Kar.) "blakkaberie" (NE), 28-VII-1920, *Pulle* 52 (U). Zanderij II, zansavanne, 16-III-1949, struik 2-3 m., vrucht groen, onrijp, "blakkaberie" (Sur.), *Lanjouw & Lindeman* 3289 (U). Zanderij II, grass savanna, frequent, shrub to 3 m., flowers white, 3-VI-1944, *Maguire & Stahel* 23654 (NY, US, U); *Maguire & Stahel* 23696 (A, NY, U, F, US, VEN). Forest of Zanderij, 31-V-1916, *Samuels* s.n. (US). Coppename R., Onobisi Kreek, 4-III-1915, *Boschwezen* 1120 (U). Plantage Berlijn, savanna, flores albi, *Focke* 1018 (isotype of *H. surinamensis*, U). Jodensavanne-Mapane Kreek area (Suriname R), op droge zadsavanne aan Blakawatre kreek, Kruiptruik als rand om hogere struik groepen, 17-XII-1954, *Lindeman* 6881 (U); op droge zandsavanne bijaan Blakawatre Kreek, Kruipstruik, bloemwit, "blakaberie" (Sur.) 17-XII-1954, *Lindeman* 6882, 6883 (U). Jodensavanne, V-1909, flores albi, *Focke* 1286 (U). Tibitisavanne; savanne bijkm. 3.1 tweede Lijn; struik 4 m.; bladen meer elliptisch, vrij spits, evenals takken witstaand, "blakaberie" (Sur.) 11-I-1949, *Lanjouw & Lindeman* 1798 (U); struik 4 m.; bladen breed en stomp, steil opgericht aan opgerichte takken, "blakaberie" (Sur.), *Lanjouw & Lindeman* 1797 (U). Patrichsavanne, 2-X-1909, *Boldingh* 3886 (U). Via secta ab Moengo tapoe ad Grote Zwiebelzwamp, in bos bij km. 15.75, boom 12 m. 17 cm. dik; bloem wit, "blakaberie" (Sur.), "merie" (Car.), 20-X-1948, *Lanjouw & Lindeman* 911 (U); it is an atypical form. Op natte zandsavanne bij Kopie, Cassewinica, struik 2-3 m. hoog, bloem wit, "blakaberie" (Sur.), 16-VII-1953, *Lindeman* 4381 (U). Savanne bij km. 100 langs spoorlijn; struik 3-4 m. hoog; vrucht groen, jong, "blakaberie" (Sur.), 16-III-1949, *Lanjouw & Lindeman* 3317 (U). Savanne, 9-VIII, *Kuypper* 568 (U); 11-X-1911, *Kuypper*, 33 (U). Without locality, *Hostman* 793 (P, BM, GH, F, MO, U); bl. wit, savanna, *Wallschlaegel* 1393 (U). *Splitgerber* s.n. (BM).

BRAZIL: Rio BRANCO: Vista Alegre, in campis, frutex floribus albis odoratis, fr. nigro edule, "umiry," *Kuhlmann* 2894 (US). AMAZONAS: Rio Içana, Tunuí, capoeira; arvore de porte muito reduzido, em cumes esteris e pedregosos, 10-V-1948, *Black* 48-2589 (IAN, NY, VEN). Rio Içana, Santana, caatinga, arvore baixa, flor branca, 2-V-1948, *Black* 48-2512 (IAN); pe da serra, terreno pedregoso, arbusto, flores, esbranquiçadas, 24-X-1947, *Pires* 754 (IAN). Manaos, Chapada, terra firme arenosa, capoeira, arvore de 5 m., flor amarelo esverdeada, perfumada, 19-VIII-1955, *INPA* 1684 (MG, US). Manaos, Strauch 1-4 m., Blumen weisslich, V-1902, *Ule* 6142 (K, MG). Alto rio Aracá, subafluente do Rio Negro, mata alta de caatinga en formação, terreno plano, solo arenoso, 30-X-1952, *Fróes & Addison* 29211 (IAN). Itaubal, Rio Aracá, 26-X-1952, *Fróes & Addison* 29102, 29096 (IAN). Rio Negro, Preto, Campina tree 25 ft. X 10 in., caatinga, white flowers, 5-XI-1947, *Fróes* 22760 (IAN, NY, U, US, VEN). Preto, Malupiry, tree 30 ft. 7 in., greenish white flower, yellow center, sweet smell, open country campina, 13-XI-1947, *Fróes* 22838 (IAN, NY, US, U); *Fróes* 22842 (IAN, NY, U). Rio Negro Aiary-pirá, rio Aiary, arvore 5 m., caatinga arenosa, 5-XI-1945, *Fróes* 21342 (IAN, F, NY, US). Alto rio Aiary, arvore pequena, flores, alvas forte cheiro agradavel, 5-XI-1945, *Fróes* 21338 (IAN, NY, US). Campo on River Paduira, 28-VI-1874, flowers white, *Traill* 80 (K). Manaos, 300 ft., tree with pale flowers slightly perfumed, VIII-1942, *Sandeman* 2199 (K). PARÁ: Lago de Fero, Praia, arbusto grande, "umiry", 20-VIII-1907, *Ducke* 8410 (BM, MG). Rio Mapuera, campinara a noreste do Tabolierinho. Arbusto, "umiry," 12-XII-1907, *Ducke* 9123 (MG).

1e. *Humiria balsamifera* var. *laurina* (Urb.) Cuatr., comb. nov.

FIGURES 21,j; 22,f,n; 24,d

Humiria floribunda var. *laurina* Urb. in Mart. Fl. Bras.12(2):439. 1877.

Humirium laurinum Klotzsch ex Urb. in Mart., ibid., as synonym.

Humiria floribunda var. *spathulata* Gleason, Bull. Torrey Club 58:374. 1931.

Type: *Schomburgk* 560, British Guiana.

Leaves elliptic-oblong, abruptly contracted into petiole at base, rounded, spatulate or obtuse at apex; entire at margin, sometimes with dotted glands beneath, glabrous; blades 3–9 cm. long, 1–3 cm. broad; petiole 5–15 mm. long. Inflorescences small, pauciflorous. Petals puberulous in the typical form, also glabrous. Young branchlets glabrous or glabrate.

H. balsamifera var. *laurina* is spread throughout the Gran Sabana of Venezuela, British Guiana, entering Colombia through the Llanos, and Brazil in some places of Pará, Mato Grosso, and Maranhão. Usually a small tree or shrub growing in open savannas or in thickets, it becomes a large tree when in the rain forest. The berries are reported to be black or purple-black when ripe and edible.

COLOMBIA: VAUPÉS: Río Paraná Pichuna, 700 ft, bush, VI-1953, *Schultes & Cabrera* 19951 (US); low bush, VI-1953, *Schultes & Cabrera* 19963 (US). Río Inírida, Raudal Alto o Mariapiri, margen derecha, 250 m. (cerro del varador), 3-II-1953, *Fernández* 2084 (COL, US), a broad-leaf form tending toward var. *guianensis*.

VENEZUELA: AMAZONAS: Esmeralda, XII-1853, *Spruce* 3419 (P, K). Esmeralda, Gran Sabana, section I, alt. 325 feet, 1-XI-1928, *Tate* 283 (NY); shrub with red berries, XI-1928, *Tate* 286 (NY, holotype of *H. floribunda* var. *spathulata* Gl.). Esmeralda, upper Orinoco, 143 m., sabana abierta; árbol pequeño 4–5 m., copa de forma irregular, tupida, tronco redondo, 10 cm., diám., corteza gris oscura, áspera, fisurada, liber color castaño claro, albura, también de tono claro, duramen de castaño a rosado fuerte o colorado; fruto ovoideo y según los nativos de color negro en la madurez y comible, “niña,” 16-V-1942, *Llewelyn Williams* 15418 (US, VEN). Between Esmeralda Savanna and southeastern base of Cerro Duida, 200 m., 22-VIII-1944, *Steyermark* 57817 (A, US, VEN). Sabana Grande, between Esmeralda and base of Cerro Duida, 175 m., abundant in savanna, shrub 0.2–2 m. tall, forming colonies, 2–5 m. across, 24-III-1953, *Maguire & Wurdack* 34677 (NY, US). Tyler-Duida expedition, rocky top of Esmeralda Ridge, small tree, 6-X-1929, *Tate* 209 (NY, US). Río Guainía, Savanna El Venado, left bank of Caño Pinichín, above Pinichín, alt. 140 m., occasional shrub, 0.3–0.7 m., 14-IV-1953, *Maguire & Wurdack* 35579 (US, NY); alt. 120–140 m., frequent, sprawling shrub to 1 m. tall, flowers greenish white, fruit green, 23-XI-1953, *Maguire, Wurdack, & Bunting* 36354 (NY, US); abundant 2 km. above Pinichín at margins of savanna, shrub sprawling to 3 m., flowers greenish white, 10-X-1957, *Maguire, Wurdack, & Keith* 41821 (NY, US). Casiquire, Río Siapa, occasionally in Sabana Hechimoni on left bank of Caño Hechimoni, shrub 0.5–2 m., flowers white, fruit dark purple, 9-II-1954, *Maguire, Wurdack, & Bunting* 37632 (NY, US). Orinoco, San Antonio, 121 m., alt., arbusto tendido de 60 cm. o mas de altura; fruto pequeño, ovoideo, verdoso; sitios arenosos en el margen de la sabana, 27-IV-1942, *Llewelyn Williams* 15052 (US).

BRITISH GUIANA: Kuyunun, IV-1842, *Schomburgk* 560 (M, holotype; NY, US, isotypes). Roraima, *Schomburgk* 628 (BM, P). Pirara, *Schomburgk* 346 (P). Parinari mountains, *Schomburgk* s.n. (K), not a typical specimen; *Schomburgk* 968 (M), not typical. Canje River, Ikuruwa Island (County Berbice), "tauroniro" (Arawak), *Forest Depart. (Hohenkerk)* 663 (K).

BRAZIL; MARANHÃO: Grajahú, beira do Rio, Campo Cerrado; arvore alta, flor amarella; a fructa é procurada pela pomba amargosa, "umiry," 13-VIII-1909, *Lisboa* 2327 (BM, MG); this collection is a puberulous form with abundant hairiness on inflorescences and the underside of leaves (midrib). PARÁ: Rio São Manoel, Posto dos Indios Caiabi, arbusto de campo, 8-I-1952, *Pires* 3877 (IAN, US). Serra do Cachimbo, 425 m., 14-XII-1956, *Pires, Black, Wurdack, & Silva* 6209 (IAN). MATTO GROSSO: Near Tabajazta, upper Machado River Region shrub on grassland, flowers white, XI-XII-1931, *Krukoff* 1483 (A, BM, NY, P, S, U).

1f. *Humiria balsamifera* var. *savannarum* (Gleason) Cuatr., comb. nov. FIGURE 21,v

Humiria savannarum Gleason Bull. Torrey Club 58:378. 1931.

Type: *Tate* 330, second sheet at NY, Venezuela, Amazonas, Esmeralda.

Leaves linear-oblong or subelliptic-oblong, narrowed-cuneate at base, sessile or subpetiolate, 5-10 cm. long, subacuminate and suddenly obtuse at apex, frequently emarginate and minutely mucronulate, the margin entire with some or no glands beneath, 5-10 cm. long, 1.5-3.5 cm. broad. Petals puberulous outside in the type specimen (the others lack flowers). Fruit oblong-ellipsoid, about 14×8 mm.

This variety is a narrow-leaf form of *H. balsamifera* found on the savannas of Esmeralda and the low Roraima Mountains. The typical leaves are narrow-sublanceolate with blunt apex and cuneate base with a 0-2 mm. long petiole. The forms with smaller and thicker leaves (e.g., *Schomburgk* 628) are transitional to variety *coriacea*.

VENEZUELA; AMAZONAS: Esmeralda, alt. 325 ft., 2-XI-1929, *Tate* 330, second sheet (NY, holotype). BOLÍVAR: Frequent on eastern slopes of Cerro Marimarota (Cerro La Puerta), 100-250 m., shrub 3-6., fruit green, 26-I-1956, *Wurdack & Monachino* 41380 (NY, US).

BRITISH GUIANA: Roraima, 1842-43, *Schomburgk* 576 (P, K). "Br. Guiana, Oct. 1842," *Schomburgk* 845 (P, K).

1g. *Humiria balsamifera* var. *parvifolia* (Juss.) Cuatr. comb. nov.

FIGURES 22,o-p; 24,e; PLATES 6-7

Humirium parvifolium A. Juss. in St. Hil. Fl. Bras. Merid. 2:89. 1829.

Humirium montanum A. Juss. in St. Hil. ibid. 2:90. 1829.

Humirium parviflorum A. Juss. in St. Hil. ibid. 2:63. 1829.

Humirium arenarium Guill. in Baill., Adansonia 1:208. 1861.

Humiria floribunda var. *parvifolia* Urb. in Mart. Fl. Bras. 12(2):438. 1877.

Humiria floribunda var. *montana* Urb. in Mart. ibid.

Type: *St. Hilaire*, Brazil, Rio de Janeiro.

Leaves small, subcoriaceous or coriaceous, glabrous, obovate, obovate-elliptic or oblong-obovate, narrowed toward the base, cuneate,

short-petiolate or sessile, rounded, truncate or very obtuse, emarginate at apex, entire or obsolete-crenulate, the secondary nerves slightly conspicuous; 1.5–4 (rarely 5) cm. long, 0.8–2.5 cm. broad. Young branchlets generally angulate or narrow-winged and hirtellous-puberulous.

There is no type cited for *Humirium arenarium* Guillemín (in schedula) as was informally described by Baillon. Several specimens of the Paris Herbarium labeled as *H. arenarium* belong to the variety *parvifolia*. The notation “M. Guillemín Cat. 205, Restingas de Tocaia, *Humirium arenarium* Nob” of one specimen must have been written by Guillemín himself, and I consider it to be the type.

This variety with small leaves is a small tree or shrub, and is frequent in “catingas,” “restingas,” and “serras” of eastern Brazil, from Pernambuco to Matto Grosso and Rio de Janeiro. St. Hilaire noted that he collected the type of *H. parvifolium* “prope urbem Cabo Frio in prov. Rio de Janeiro” and the type of *H. montanum* “prope vicum Itambe in montibus provinciae Minas Geraes” (pp. 89–90). Curiously, the same variety (or a very close form) has been found in eastern Peru.

BRAZIL: PERNAMBUCO: Recife, fazenda Modelo Tigipió, arbusto pequeno, flores alvo crema perfumadas, 12–III–1950, *Lima* 1623 (IAN). GOIÁS: Serra dos Viadinhos, arvore pequena na margen do um corrego, IX–1892, *Glaziov* 63 (P). BAHIA: “Circa Bahiam,” *Blanchet* 1005 (NY, BM); *Blanchet* 3144A (P). “In Provincia Bahiae,” *Blanchet* 3570 (BM, P). Serra de Acurua, *Blanchet* 2810 (F, BM, NY, US, paratypes of *H. montanum*). Rio San Francisco, *Blanchet* s.n. (GH). Saubino, Jacobin, *Blanchet* 3422 (US, F, paratypes). Inter Vitoria et Bahia, *Sellow* 2212, 2228, 180 (NY, US, S, BM). Bompui, *Curran* 159 (Y). Inter Campos et Victoria, *Sellow* s.n. (K). MINAS GERAIS: “Minas, septembre fl.,” St. Hilaire s.n. (P, isotype of *Humirium montanum* Juss.). Cocais, arvor da Serra, flor alva, *Hoehne* 7970 (NY). Chiribiry, arbrisseau, fleurs blanchâtres, 29–III–1892, *Glaziov* 18962 (P). Serra do Cipó, km. 132, arvore pequena, 6–IV–1951, *Black & Magalhães* 51–11790 (IAN). Serra do Cipó, 16–I–1951, *Pires & Black* 2961 (IAN). Catingas de Tocaia, XII–1838, “*Humirium arenarium* Nob. medium inter *H. montanum* et *H. parvifolium*,” *Guillemín* 205 (P, type of *Humirium arenarium* Guill.). RIO DE JANEIRO: No locality, St. Hilaire 114/5 (P, isotype of *Humirium parvifolium* Juss.). Rio de Janeiro, *Glaziov* 10342 (P). Rio de Janeiro, Herb. Brogniard, *Herb. Richard*, (P, S). Rio de Janeiro, *Glaziov* s.n. (S). Restinga de Maua, 2–V–1891, arbrisseau très touffu, *Glaziov* 18180 (P, F, US, NY); *Glaziov* 8286 (A, P, S). Mauá, 15–XII–1874, *Glaziov* 7765 (P). Restinga da Tijuca, 25–XI–1866, *Glaziov* 731 (P), 29–VII–1872; *Glaziov* 6196 (US, P). Cabo Frio, Praia do Pontal, ao nível do mar, 17–IV–1952, *L. B. Smith* 6694 (US). Cabo Frio, 19–IX–1881, *Glaziov* 12515. (NY, UC, P). Cabo Frio Co., Arraial do Cabo, Pontal Beach, 1953, *Segadas-Vianna, et al.* I–1383 (US); II–III–1951, *Mello Filho L. E.* 1186; restinga, 3–VI–1953, arbore 3 m., calice branco esverdeado, corola branca, *Segadas-Vianna, et al.* I–439 (US); na fimbria de moita da restinga interna, 13–VIII–1953, substratum arenoso, arbusto 1 m., caliz verde, petalos brancos, *Segadas-Vianna et al.* I–821 (US); na restinga interna, 24–V–1953, substratum arenoso, plano, mesofanerofita comun, en colonias, arbusto ramificado da base em moita arredondada de 1.50 a 2 m., calice verde, corola branca, estambres filete branco, antera branca.,

Segadas-Vianna et al. I-310 (US). Casimiro de Abreu Co., District of Barra de São João, near Barra de São João Village, restinga interna, 3-IX-1953, calice verde, corola 5 petalos, branca, estames filete branco, antera branca, *Segadas-Vianna et al.* I-907 (US); 5 km. north of Rio das Ostras borough, 5-IX-1953, *Segadas-Vianna et al.* I-1416 (US); 1 km. ao sul do Povoado de Rio das Ostras, inland restinga, 28-V-1953, *Segadas-Vianna et al.* I-369 (US); 3 km. norte do Povoado de Rio das Ostras, nas moitas ou isolada na restinga interna, *Segadas-Vianna et al.* I-385 (US); 5 km. ao norte do Povoado de Rio das Ostras, 29-V-1953, na restinga arborescente ate 5 m., 4-IX-1953, *Segadas-Vianna et al.* I-945 (US). Distrito Federal, Restinga de Itapeba, Recreio dos Bandeirantes, 1-X-1950, ao nivel do mar, *Segadas-Vianna* 3506 (US); 29-X-1950, *Segadas-Vianna* 3634, 3635 (US). Recreio dos Bandeirantes, XI-1931, *Lutz* 681 (US); 22-X-1938, *Alston & Lutz* 169 (BM). Praia de Sernambetiba, ao nivel do mar, 4-IX-1952, *L. B. Smith* 6406 (NY, US). Rio de Janeiro, 1836, *Gomes* s.n. (K). Tocojá, "Herbarium Zuccarinii, comm. M. C. Vendob, anno 1809, legit in Brasilia Dr. Pohl," *Pohl* s.n. (M). Macahé, 1845, *Herb. John Miers* 8915 (BM). Without locality, *Riedel* s.n. (GH, K, M, P, US); *Riedel* 3570 (U, S, in part).

PERU: SAN MARTÍN: Zepalacio, near Moyabama, alt. 1,100 m., mountain forest, tree 8 m., flowers pale yellow, VIII-1934, *Klug* 3706 (A, GH, BM, F, MO, NY, S, US). In monte Campana prope Tarapoto orientalis, VIII-1856, *Spruce* 4335 (GH, BM, S).

1h. *Humiria balsamifera* var. *coriacea* Cuatr., var. nov.

FIGURES 21,*o-r*; 22,*i-l*; 23,*e-g*; 24,*b*; PLATE 8

Arbuscula vel arbor 4-8 m. alta ramosa ramulis terminalibus crassis nitidis minute hirtis-puberulis vel glabris.

Folia crassa rigideque coriacea. Lamina obovata vel obovato-elliptica apice rotundata vel obtusa breviter emarginata et in sinu mucronulata, basi cuneata subite vel gradatim in pseudopetiolum alatum 2-6 mm. longum attenuata cuneata, margine integra plana eglandulosa vel paucis glandulis, 4-7 cm. longa, 2.4-5.2 cm. lata, utrinque glabra supra viridis nitidula nervo medio signato secundariis obtuse prominulis venulis reticulatis paulo vel haud conspicuis; subtus costa crassa elevata nervis secundariis circa 4-5 mm. inter se distantibus subparallelis prope marginem arcuato-anastomosatis nervis minoribus parallelis et venulis prominulis anastomosato-reticulatis.

Inflorescentiae cymoso-paniculatae corymbiformes subterminales et axillares folia aequilongae vel breviores, axi ramulisque angulosi vel hirtis-puberuli; bracteis late ovatis ovato-triangularibus subacutis vel obtusiusculis amplexicaulibus inferioribus ad 2 mm. longis superioribus 1 mm. longis crassiusculis glabrisque. Ramusculi cymorum ultimi crassi angulati hirtulo-puberuli breves ad 1 mm. longi. Pedicelli crassi glabri 0.5-1.5 mm. longi. Calyx cupularis circa 1 mm. altus crassus; sepalis usque ad medium coalitis depresso-rotundatis glabris margine minutissime ciliatis excepto. Petala 5 libera, crassiuscula oblonga subacuta glabra circa 5 mm. longa 1.4 mm. lata. Stamina filamentis 3-4.5 mm. longis infra medium in tubum glabrum coalitis parte libera minute papillosis; connectivo antheris oblongo linguiformi subacuto

0.8 mm. longo thecis orbicularibus barbatisque. Squamae disci 20 crassiusculae in tubulum argute dentatum coalitae. Ovarium obovatum glabrum vel apice leviter pilosum 5-loculare loculis 2 ovulis superpositis pendulis. Stylus 3–4 mm. longus hirtulus. Stigma capitatum 5-lobatum. Drupa oblongo-ellipsoidea 10–14 mm. longa 5–8 mm. crassa, exocarpio carnosio. Endocarpium durum circa 10×5 mm. 10-striatum sublaeve apice leviter attenuatum 5-foraminatum.

Type in the U.S. National Herbarium, No. 1901203, collected in rocky soil at Mureyena Falls, alt. 800 m., State of Bolívar, Venezuela, October 10, 1946, by Félix Cardona, No. 1823. Isotypes in the Herbarium of the New York Botanical Garden and in the Instituto Botánico of Venezuela, Caracas. Paratype at U.S. National Herbarium, No. 1909308, collected at Río Caroní, Bolívar, Venezuela, by Félix Cardona, No. 1768.

Shrub or small tree with hirtellous or puberulous, sometimes glabrate, young branchlets. Leaves thick and rigid, coriaceous, glabrous, obovate or obovate-elliptic, rounded or obtuse, emarginate and mucronulate at apex, attenuate in winged, 2–6 mm. long petiole at base, midrib prominent beneath, the secondary nerves and reticulum slightly conspicuous or obsolete above, prominulous beneath; 4–7 cm. long, 2.4–5.2 cm. broad. Branchlets of the inflorescence hirtellous-puberulous, the pedicels (0.5–1.5 mm. long) glabrous. Calyx cupular, glabrous except for the ciliate margin. Petals oblong, subacute, glabrous. Style 3–4 mm. long, hirtellous. Drupe oblong-ellipsoid, $10\text{--}14 \times 5\text{--}8$ mm., the endocarp 10×5 mm., striate, 5-foveolate at apex.

The rigid sclerophyllous texture of the leaves, and their shape and size are the most distinctive characters of this variety, which seems to conform to the most xerophytic conditions of the sandstone and granitic hills of the savanna.

H. balsamifera var. *coriacea* is endemic to the Guiana hills where it is very common. It is a characteristic tree or shrub of the vegetation of these mountains, it being found often abundantly on the slopes and at the top of the hills where it forms actual stands. It is also a constituent of the open savanna vegetation. It is especially found at between 700 and 2,000 m. elevation, but it is present at much lower altitudes (as, e.g., 350 m.).

VENEZUELA: AMAZONAS: Cerro Duida, Río Cunucunuma, Culebra Creek drainage, alt. 1,500 m., tree to 5 m., flowers white, 19–XI–1950, *Maguire, Cowan, & Wurdack* 29541 (NY, US). Ridges of Caño Negro Basin, alt. 2,000–2,300 m., abundant in scrub sabana, tree 4 m., flowers white, 23–XI–1950, *Maguire, Cowan, & Wurdack* 29697 (NY, US). Cerro Duida, Savanna Hills; alt. 1,020–1,200 m.; shrub 10–15 feet tall, leaves coriaceous, dark green above, dull green below; fruit blackish, flowers greenish, *Steyermark* 58288 (NY, US). Summit of Savanna

Hills, bushy tree, *Tate* 733 (NY, US). Cerro Sipapo (Paráque), savanna breaks, Peak 1, alt. 2,000 m., shrub or small tree, 12-XII-1948, *Maguire & Politi* 27627 (US, NY); frequent in marsh at savanna camp, alt. 1,500 m., much branched shrub to 4 m. tall, 15-XII-1948, *Maguire & Politi* 27695 (NY, US). Serranía Yutaje, Río Manapiare, cerro Coro-Coro, frequent in savannas, alt. 1,500 m., rounded shrub 1-3 m. tall, flowers white, 2-III-1953, *Maguire & Maguire* 35453 (NY, US). Cerro Yutaje, occasional in scrub forest on northwest ridge, alt. 1,400 m., bushy rounded tree 2-5 m. tall, flowers white, 11-II-1953, *Maguire & Maguire* 35140 (NY, US). Cerro Yapacana, frequent on summit at alt. 1,200 m., tree to 5 m., flowers white, 2-I-1951, *Maguire, Cowan, & Wurdack* 30622 (US, NY); this tree is a form having smaller leaves, but it can hardly be separated from var. *coriacea*. Río Cunucunuma, Cerro Huachamacari, summit camp at alt. 1,800 m., occasionally near camp, much branched tree 8 m., flowers white, 6-XII-1950, *Maguire, Cowan, & Wurdack* 30018 (NY, US). Río Ventuari, Serranía Parú, Río Parú, Caño Asisa, alt. 2,000 m., occasionally on summit along west rim, tree 3 m., flowers white, 7-II-1951, *Cowan & Wurdack* 31301 (NY, US); bushy tree 2 m., buds turning white, 31-I-1951, *Cowan & Wurdack* 31090 (NY, US); abundant in open areas in cumbre, alt. 1,800 m., shrub 1 m., flowers greenish, *Kathleen Phelps & Hitchcock* 508 (NY). Cerro Moriche, frequent in cumbre at alt. 1,250 m., 15-I-1951, *Maguire, Cowan, & Wurdack* 30918 (NY, US); frequent in montane savanna at alt. 800 m., tree 5 m., fruit turning brown-red, 14-I-1951, *Maguire, Cowan, & Wurdack* 30885 (NY, US). BOLIVAR: Gran Sabana, between waterfall at Rue-meru and Divina Pastora on Río Cuquenán north of Santa Elena, south of Mount Roraima, alt. 1,065 m., dry sandy upland; shrub 4-6 ft. tall; leaves subcoriaceous, deep green above, pale green below; petals white; *Steyermark* 59186 (NY, US, VEN). Río Caroní, playas rocosas, aguas arriba del salto Eutouamini, 720 m. alt.; árbol 5 m., flores gris claro, *Cardona* 1768 (US, paratype). Río Caroní, lugares rocosos frente a los raudales Mureyena, 800 m. alt., árbol 6 m., flor amarilla, 10-X-1946, *Cardona* 1823 (US, holotype; NY, VEN, isotypes). Río Caroní, cumbre del cerro Acopán, 2,200 m. alt., arbusto 6 m., X-1947, *Cardona* 2269 (US). Lomas pedregosas entre el Cerro Peraí y las fuentes del río Uaiparú afluente del Icabarú, 900 m., alt. árbol 5 m., flores blancas, 20-X-1946, *Cardona* 1869 (NY, US). Lomas pedregosas del río Icaburú, 460 m., arbusto 4 m., V-48, *Cardona* 2533 (VEN). Sabanas de Icaburú, hacia El Caribe, 450-850 m. alt., árbol aislado 10 m., flores blancas, 22-XII-1955, *Bernardi* 2603 (VEN). Alto Caroní, río Carrao, 350 m. alrededores Salto Hacha, 350 m. alt., en playas, arbolito 4 m., *Cardona* 2877 (US, F). Auyantepuí, 2,100 m., alt. arbusto 4 m., I-1949, *Cardona* 2670 (NY). Mount Auyan-Tepuí, 1,100 m. alt., *Tate* 1113 (NY, VEN). Auyantepuí, campamento de Guayaraca 1,100 m., alt. crecen en Barbacenetum, formación seca arbustiva, cerca del campamento, IV-1956, *Vareschi & Foldats* 4563, 4573 (VEN). Chimantá Massif, Torono-tepuí, summit along Caño Mojado, between base of upper falls and drop to escarpment at alt. 1,895-1,910 m., tree 4 m., buds green, flowers greenish white, fruit green, locally frequent, 23-II-1955, *Steyermark & Wurdack* 1109 (NY, US). Alto Río Paragua, Cerro Perro, in sandstone savannas, *Cardona* 774 (NY, US, VEN). Cerro Bolívar, frequent on summit of West Peak at alt. 750 m., rounded much-branched small tree, flowers white, 2-XII-1951, *Maguire* 32686 (NY, US). Cerro Bolívar, Ciudad Piar, 750 m. alt.; variable desde arbusto 2 m. a árbol de 8-12 m., siempre muy ramificado, tronco libre muy corto; es una de las especies características del tope del Cerro Bolívar IV-1954, *Aristeguieta* 2174 (VEN). SUCRE: Lago de Guanoco, crece en pequeñas islas formadas por el levantamiento del suelo, arbusto, flores blancas, VIII-1955, *Lasser & Vareschi* 3888 (VEN).

BRITISH GUIANA: Kaietur Plateau, from bush island, in savanna, frequent, bushy crowned tree 4–6 m., 4–8 cm., flowers greenish white, 8–V–1944, *Maguire & Fanshawe* 23295 (NY, U, US, VEN). Kaietur Plateau, Potaro River, on sandstone flat in the open, alt. 1,300 ft., a tree 12 ft., calyx green, corolla greenish white, *Altson* 545 (K, P); tree 20 ft. IX–X–1881, *Jenman* 1023 (K).

SURINAM: Tafelberg, vicinity Camp No. 1, savanna, alt. 300 m., shrub 4 m., much-branched and rounded, flowers white, 4–VIII–1944, *Maguire* 24223 (NY, US, U, VEN). Tafelberg, Savanna No. II, frequent, shrub to much-branched rounded tree of 7 m. height, 12–IX–1944, *Maguire* 24707 (NY, U, US). Savanna VII, common shrub or rounded, much-branched-tree to 10 m., 25 cm. diam., 17–IX–1944, *Maguire* 24789 (NY, U, US). Savanna VIII, frequent shrub or bushy small tree to 8 m., 10 cm. diameter, flowers white, extensive rock and pigmy bush openings, alt. 776 m., 23–VIII–1944, *Maguire* 24443 (NY, US, U).

BRAZIL: Rio BRANCO: Serra Tepequén, dominant on unburnt portion of rim, alt. 1,000–1,200 m., bushy rounded tree, 5–8 m. tall, leaves glossy green, flowers white, 4–XII–1954, *Maguire & Maguire* 40159 (NY, US). Região entre o Rio Maú e o Canan, arvore de flor esverdeada, 22–XI–1954, *INPA* 620 (MG).

li. *Humiria balsamifera* var. *guaiquinimana* Cuatr., var. nov.

FIGURE 21,*w*; 24,*a*; PLATE 9

Arbor parva usque 8 m. alta ramulis terminalibus crassis minute hirto-pubescentibus deinde glabris griseis fissuratis nitidis. Folia crasse rigideque coriacea subsessilia. Lamina suborbiculato-elliptica vel suborbiculata apice rotundata vel obtusissima saepe retusa et emarginata in sinu longe mucronata, basi subite lateque cuneata subpetiolata contracta, margine integra plana eglandulosa, 4–7 cm. longa 3–5.2 cm. lata, utrinque glabra supra viridis nitidula nervo medio signato secundariis obtuse prominulis venulis reticulatis paulo conspicuis; subtus costa crassa elevata nervis secundariis prominulis circa 4–5 mm. inter se distantibus subparallelis prope marginem arcuato-anastomosatis nervis minoribus parallelis et venulis prominulis anastomosato-reticulatis.

Inflorescentiae cymoso-paniculatae subterminales et axillares folia breviores, axi ramulisque angulosi pubescentes; bracteis late ovatis amplexicaulibus inferioribus ad 3 mm. longis superioribus 1 mm. longis crassiusculis glabrisque. Ramusculi cymorum ultimi crassi pubescentes breves ad 1 mm. longi. Pedicelli brevissimi circa 0.5 mm. longi. Calyx circa 1.2 mm. longus; sepalis usque ad medium coalitis rotundatis glabris margine minutissime ciliatis excepto. Petala 5 libera, elliptico-oblonga crassa glabra in alabastro 3.5 mm. longa. Stamina basi in tubum glabrum coalita, parte libera minute papillosa; connectivo antheris ovato compresso, thecis orbicularibus barbatisque. Ovarium glabrum apice leviter piloso excepto.

Type in the U.S. National Herbarium, No. 1878323, collected at Cerro Guaiquinima at the headwaters of Río Paragua, alt. 1760 m., in the State of Bolívar, Venezuela, July 15, 1944, by Félix Cardona (No. 1112).

Small tree with thick, hirtellous terminal branchlets becoming glabrous. Leaves thick, rigid-coriaceous, glabrous, subsessile, suborbiculate-elliptic or suborbicular, rounded or very obtuse at apex, often retuse and emarginate, and mucronate, abruptly attenuate, subpetiolate-cuneate at base, the margin flat, entire, eglandular, the midrib prominent beneath, secondary nerves and reticulum prominulous beneath. Petals elliptic-oblong, glabrous. The thick, stiff, glabrous, elliptic or suborbicular leaves only very shortly, abruptly cuneate-contracted at base (pseudopetiole 1–2 mm. long) and hirtellous young branchlets differentiate this variety, which is restricted to Mount Guaiquinima.

VENEZUELA: BOLÍVAR: Alto Río Paragua, Cerro Guaiquinima, alt. 1,760 m., 15–VII–1944, *Cardona* 1112 (US, holotypus); alt. 1740 m., X–1943, *Cardona* 965 (F, NY). Cerro Guaiquinima, dominant in quebradas near Cumbre Camp, alt. 1,800 m., densely rounded tree to 8 m. tall, leaves glossy, 25–XII–1951, *Maguire* 32763 (NY, US); rounded tree 3–10 m. tall, dominant along west escarpment, alt. 1,800 m., 14–IV–1952, *Maguire* 33099 (NY, US).

1j. *Humiria balsamifera* var. *stenocarpa* Cuatr., var. nov.

FIGURES 21,*s–t*; 23,*n*

Arbor 3–8 m. alta ramulis juvenilibus glabris. Folia tenuiter coriacea rigidiuscula glabra; lamina obovato-elliptica apice rotundata vel obtusissima breviterque emarginata et mucronulata, basi subite cuneata in petiolum alatum 5–7 mm. longum attenuata, costa prominenti nervis secundariis plus minusve prominulis, margine integra vel levissime remoteque crenata sparsis glandulis vel eglandulosa; 3–5.5 cm. longa 2–3.6 cm. lata. Petala glabra oblongo-attenuate circa 6×1.5 mm. Ovarium glabrum, parcis pilis apice exceptum. Drupa oblonga apice subacuta 11–14 mm. longa 4–5 mm. crassa in sicco, exocarpio tenui; endocarpio oblongo utrinque obtuso 11–13.5 mm. longo 3.8–4.8 mm. crasso, longitudinaliter 10-striato apice minute 5-foraminato.

Type in the U.S. National Herbarium, No. 2270239, collected on Serra Tepequen, in Rio Branco, Brazil, dominant on rocky slopes at alt. 1,000–1,200 m., November 29, 1954, by Bassett and Celia Maguire (No. 40105). Isotype in the Herbarium of the New York Botanical Garden.

Small much-branched or bushy tree with glabrous branchlets. Leaves subcoriaceous rather stiff, glabrous, obovate-elliptic, rounded or very obtuse and emarginate at apex, cuneate at base and attenuate into petiole 5–7 mm. long; midrib prominent, minor veins more or less prominulous; 3–5.5 cm. long, 2–3.6 cm. broad. Petals glabrous, oblong-attenuate toward the apex. Drupe oblong, subacute, 11–14 mm. long 4–5 mm. thick when dry, endocarp oblong, obtuse at both ends, 11–13.5 mm. long, 3.8–4.8 mm. thick, with 10 thin longitudinal

striations and 5 minute foveae at apex. Very closely related to variety *coriacea*, it primarily differs in its cylindrical, oblong, narrow endocarp and its thinner and longer attenuate leaves.

VENEZUELA: BOLÍVAR: Cerro Altamira, 10 km. east of Ciudad Piar, alt. 425–650 m., frequent, bushy tree 3–8 m., flowers greenish white, fruit green, 19-X-1953, *Maguire, Wurdack, & Bunting* 35882 (NY, US).

BRAZIL: Rio BRANCO: Serra Tepequena, alt. 1,000–1,200 m., dominant on rocky slopes, rounded tree 3–8 m. tall, flowers white, 29-XI-1954, *Maguire & Maguire* 40105 (US, holotype; NY).

1k. *Humiria balsamifera* var. *imbaimadaiensis* Cuatr., var. nov.

FIGURE 22,*m*

Frutex ad 30 cm. alta, ramulis glabris. Folia crasse rigideque coriacea sessilia glabra; lamina elliptica apice rotundata sed anguste emarginata in sinu mucronulata, basi rotundata vel subtruncata plus minusve auriculata amplexans, margine integra subtus paucis glandulis vel eglandulosa, 2.5–5 cm. longa. 1.7–3.2 cm. lata, costa subtus eminenti basim versus crassa, nervis secundariis venulisque praesertim subtus prominulis. Inflorescentiae folia subaequantur pilis minutissimis patulis sparsis munitae. Petala oblonga obtusiuscula circa 4 mm. longa 1.2 mm. lata dorso sparsis pilis patulis reliqua glabra. Ovarium glabrum apice paulo piloso excepto. Drupa ellipsoidea, specimine unico vidit 7×5 mm.

Type in the U.S. National Herbarium, No. 2270222, collected at the Imbaimadai savannas, alt. 550 m., along the Upper Mazaruni River in British Guiana, October 21, 1951, by Bassett Maguire and D. B. Fanshawe (No. 32158). Isotype in the Herbarium of the New York Botanical Garden.

Low shrub with glabrous terminal branchlets. Leaves thick, rigid-coriaceous, sessile, glabrous, elliptic, rounded and emarginate (sinus mucronulate) at apex, rounded or subtruncate and more or less auriculate, amplexant at base, margin entire; 2.5–5 cm. long, 1.7–3.2 cm. broad, midrib prominent beneath, secondary nerves and veins prominent, chiefly beneath. Petals oblong, subobtusate, about 4 mm. long, with very few hairs outside. Drupe ellipsoid about 7×5 mm. It differs from related variety *coriacea* in its elliptic, sessile, basally rounded, subauriculate and amplexant leaves; it is, furthermore, a low, depressed shrub and has shorter petals with few hairs outside.

BRITISH GUIANA: Upper Mazaruni River, Imbaimadai savannas, alt. 550 m., frequent, depressed shrub to 3 dm. tall and 1 m. across; leaves stiff, leathery; flowers greenish white, 21-X-1951, *Maguire & Fanshawe* 32158 (US, holotype; NY, isotype).

1l. *Humiria balsamifera* var. *iluana* Cuatr., var. nov.

Arbuscula usque ad 8 m. alta ramulis terminalibus glabris. Folia crassiuscule rigideque coriacea glabra; lamina obovato-elliptica apice

paulo attenuata obtusa emarginulata minuteque mucronulata, basi cuneata in latum petiolum alatum crassum 5–7 mm. longum attenuata, margine integra raris minutis glandulis; costa conspicua subtus inferne crassa, nervis secundariis crebris venulisque utrinque prominulis; 3.5–7 cm. longa 1.8–4 cm. lata. Petala lineari-oblonga subacuta 5.5–6 mm. longa, circa 1.2 mm. lata extus hirtula, pilis sparsis patulis praedita. Ovarium apice parvis pilis exceptis glabrum. Drupa oblongo-ellipsoidea basi rotundata, apice obtusiuscula 10–12 mm. longa 6–6.5 mm. crassa, exocarpio carnosio in sicco tenui; endocarpio striatulo.

Type in the U.S. National Herbarium, No. 2270225, collected on Mount Ilu-tepuí, alt. 1,400 m., at Gran Sabana, in the State of Bolívar, Venezuela, March 13, 1952, by Bassett Maguire (No. 33388). Isotype in the Herbarium of the New York Botanical Garden. Paratype in the Herbarium of the New York Botanical Garden, collected between Uarapata and Enemasio at Gran Sabana, Bolívar, Venezuela, February 8, 1952, by Bassett Maguire (No. 33242).

Small bushy tree or shrub with glabrous terminal branchlets. Leaves thick, stiffly coriaceous, glabrous, obovate-elliptic, slightly attenuate and obtuse at apex, more or less emarginate and mucronulate, cuneate at base and attenuate into 5–7 mm. long petiole; midrib prominent beneath, secondary nerves and veins prominulous on both sides; 3.5–7 cm. long, 1.8–4 cm. broad. The petals linear-oblong, subacute, sparsely hirtellous outside. Drupe oblong-ellipsoid, rounded at base, rather obtuse at apex, 10–12 mm. long, 6–6.5 mm. thick. Variety *iluana* essentially differs from variety *coriacea* in its hirtellous petals.

VENEZUELA: BOLÍVAR: Gran Sabana, Ilu-tepuí, between Uarapata and Enemasio, common in savannas, alt. 1,000 m., bushy tree or shrub 1–6 m. tall, 8–II–1952, *Maguire* 33242 (NY, paratype); alt. 1,400 m. near Camp 1, occasional in low open woodland, rounded tree 8 m., 13–III–1952, *Maguire* 33388 (US, holotype; NY, isotype).

lm. *Humiria balsamifera* var. *pilosa* (Steyermark) Cuatr., comb. nov.

Humiria pilosa Steyermark, Fieldiana Bot. 28:270. 1952.

FIGURE 24, f

Type: *Steyermark* 60289, Venezuela, Bolívar, Ptari-tepuí.

Leaves coriaceous, oblong-elliptic, attenuate very little at both ends, subrounded or obtuse at apex, commonly emarginate and mucronulate in depression, narrowed to short, winged petiole (2–3 mm. long), entire or slightly crenulate at margin with few minute glands or eglandular; 3–5 cm. long, 1.5–2.5 cm. broad; above glabrous, lustrous, smooth with conspicuous midrib; beneath with prominent, hirtellous midrib, elsewhere puberulous or glabrous, secondary nerves and veins prominulous. Branchlets of inflorescence and pedicels

hirtellous. Sepals and petals hirtellous outside. Ovary glabrous. Young branchlets hirtellous-pubescent or hirtellous-puberulous.

Primarily the hirtellous character of the branchlets, pedicels, calyx, petals, and leaves beneath distinguishes this variety. *Steyermark* 59621, which undoubtedly belongs to the same taxon, has a scarcer indument on leaves and branchlets.

VENEZUELA: BOLÍVAR: Ptari-tepuí, scrubby forest on rocky portion of plateau on southeast facing slopes, alt. 1,600 m.; shrub 10 ft. tall; leaves chartaceous to subcoriaceous, dark green above, dull paler green below; fruit edible, oblong, dull purple-red or blackish red, 1-XI-1944, *Steyermark* 59621 (F, NY). Vicinity of Misia Kathy Camp on mesa between Ptari-tepuí, alt. 1,615 m.; tree 40 ft; leaves coriaceous, deep green above, paler green below; rich woods, *Steyermark* 60289 (holotype F, isotype NY).

In. *Humiria balsamifera* var. *minarum* Cuatr., var. nov.

Arbuscula ramulis terminalibus glabris. Folia tenuiter coriacea rigidula glabra. Lamina oblongo-elliptica utrinque attenuata apice angustata subacuta mucronulata interdum minute emarginata, basi angustata in brevem petiolum 1–2 mm. longum, margine minute crenulata et subtus glandulosa; supra tantum costa conspicua; subtus costa prominenti nervis secundariis et venulis laxe reticulatis prominulis; 3–5.5 cm. longa 1.5–2.4 cm. lata. Inflorescentiae folia subaequales vel breviores, ramulis parcissime pilosulis. Pedicelli (circa 1.5 mm.) et calyx glabri. Petala glabra oblonga apicem versus angustata subacuta 5.5–6 mm. longa basi 1.6 mm. lata. Ovarium apice piloso excepto glabrum.

Type in the U.S. National Herbarium, No. 1592630, collected on the slope of Serra do Rio Grande, at 1,280 m., near Diamantina, State of Minas Geraes, Brazil, May 12, 1931, by Ynes Mexia (No. 5815).

Shrub with glabrous terminal branchlets. Leaves thin-coriaceous, rigidulous, glabrous, oblong-elliptic, attenuate at both ends, narrowed, subacute and mucronulate (sometimes emarginate) at apex; petiole 1–2 mm. long; margin minutely crenate, glandular-punctate beneath; midrib prominent beneath, secondary and lax-reticulate veins prominent; 3.5–5 cm. long, 1.5–2.4 cm. broad. Pedicels and calyx glabrous. Petals glabrous, oblong, subacute at apex.

This variety is very closely related to varieties *coriacea*, *parvifolia*, and *pilosa*; it is distinguished by its elliptic, subcoriaceous leaves, which are finely crenulate and glandular beneath and attenuate at apex; furthermore, it is completely glabrous except for the very sparse minute hairs at the inflorescence.

BRAZIL: MINAS GERAES: Diamantina, slope of Serra do Rio Grande, alt. 1,280 m., among rocks near seepage, shrub 1.5 m., slightly fragrant, greenish white flowers, Y. Mexia 5815 (US, holotype; A, BM, NY, S, GH, U, isotypes).

Moist plains near Cidade Diamantina, shrub about 4 ft. high, VIII-1840, *Gardner* 4452 bis (BM). No locality, *Riedel* s.n. (M, S part).

2. *Humiria fruticosa* Cuatr., sp. nov.

FIGURE 24,*g-h*

Frutex ramosus ad 1 m. alta ramulis griseis vel cinereis minute hirtello-pubescentibus.

Folia brevia coriacea rigida sessilia glauca. Lamina subelliptico-oblonga vel oblonga, basi subcordata vel rotundata amplexans raro paulo attenuata obtusaque, apice leviter attenuata obtusa mucronulata, margine integerrima subtus inferne plerumque 3 minutis glandulis utroque latere reliqua eglandulosa, 1.5-4 cm. longa, 0.5-1.5 cm. lata; supra pallido-viridis laevis costa pallida tantum notata minutissimis pilis acutis patulis copiosis praedita; subtus densiuscule patulo-pilosula costa elevata nervis secundariis circa 10 utroque latere paulo ascendentibus paulo prominulis prope marginem curvato-anastomosatis venulis laxe reticulatis leviter vel haud prominulis conspicuisque.

Inflorescentiae axillares foliis breviores plerumque 3-4 florum, pedunculo 0.5-1.4 cm. longo erecto striolato paulo compresso minute patulo-piloso, ramulis 1-3 mm. longis rigidis angulatis minute pilosis. Bractae ovato-triangulares acutae vel ovato-lanceolatae, 0.6-1.5 mm. longae minute patulo-pubescentes. Pedicelli 1-2 mm. longi sparse puberuli sursum incrassati. Sepala triangulari-ovata subacuta crassa 1-1.2 mm. longa extus sparse pilosula margine dense ciliata. Petala aestivatione quincuncialia, linearia ad apicem attenuata apice subacuta brevissime mucronulata, crassiuscula sursum dorso minutissimis pilis sparsis munita reliqua glabra, circa 6 mm. longa 1.3-1.5 mm. lata. Stamina 20 filamentis crassiusculis papillois inaequilongis, 3-4.5 mm. longis, tertio inferiore in tubum coalitis. Antherae 1.2-1.4 mm. longae connectivo crasso lanceolato acutiusculo glabro 0.9-1 mm. longo, thecis ellipsoideis basalis barbatis circa 0.4 mm. longis. Discus intrastaminalis crassiusculus dentatus circa 0.8 mm. longus. Ovarium ovatum apice paulo piloso ceterum glabrum, 1.5 mm. altum 5-loculare loculis biovulatis, ovulis ellipsoideis in loculo superpositis. Stylus circa 3 mm. longus robustus erectus dense hirtus. Stigma 5-capitato-lobatum.

Type in the U.S. National Herbarium, No. 2270237, collected at the base of Cerro Yapacana, alt. 125 m., savannas, in the State of Amazonas, Venezuela, November 20, 1953, by Bassett Maguire, John Wurdack, and George Bunting (No. 36580). Isotype in the Herbarium of New York Botanical Garden.

Sprawling shrub up to 1 m. high with spreading branches and minutely hirtellous-pubescent branchlets. Leaves small, coriaceous, rigid, sessile. Blade subelliptic-oblong or oblong, subcordate or rounded at base, amplexant, slightly attenuate, obtuse and mucronulate at apex, margin entire and mostly with three small glands near

base on lower side; 1.5–4 cm. long, 0.5–1.5 cm. broad; nearly smooth above with abundant minute, pointed, spreading trichomes, pale midrib conspicuous, other nerves obsolete; densely covered beneath with minute, patulous trichomes, midrib prominent, 9–10 pairs of secondary nerves slightly prominulous, somewhat ascending, curvate-anastomosate near margin, veins lax-reticulate, slightly or not at all conspicuous.

Inflorescence axillary, shorter than leaves, usually bearing 3–4 flowers, peduncle 0.5–1.4 cm. long, compressed, striate, minutely spreading-pubescent, branchlets 1–3 mm. long, angulate, minutely pilose. Bracts ovate-triangular or ovate-lanceolate, 0.6–1.5 mm. long, minutely spreading-pilose. Pedicels 1–2 mm. long, sparsely puberulous, thickened toward top. Sepals triangular-ovate, subacute, thick, 1–1.2 mm. long, sparsely pilose outside, margin densely ciliate. Petals linear, white, attenuate, subacute and mucronulate, with scarce, minute hairs outside near apex, about 6 mm. long, 1.3–1.5 mm. broad. Stamens 20, filaments rather thick, papillose, 3–4.5 mm. long, united in tube on lower third. Anthers 1.2–1.4 mm. long with lanceolate, subacute, 0.9–1 mm. long connective; thecae basal, ellipsoid, hairy, about 0.4 mm. long. Disk about 0.8 mm. high, dentate. Ovary ovoid, only scarcely pilose at apex, 5-locular, cells biovulate, ovules ellipsoid, superimposed inside cavities. Style about 3 mm. long, erect, densely hirtellous. Stigmas 5, capitate-lobate.

H. fruticosa is very distinct from all other species by its shrubby habit, its longer subacute sepals, its small, narrow, sessile leaves, and its fine pubescence of minute, patulous, pointed trichomes, which more or less densely cover the branchlets, inflorescences, and leaves.

This species is highly endemic and well defined, and is limited to the savannas around the Guiana hill called Cerro Yapacana.

VENEZUELA: AMAZONAS: Orinoco, Cerro Yapacana, Savanna No. 3, alt. 125 m., northwest base of mountain, frequent, weak shrub to 1 m., 31–XII–1950, *Maguire, Cowan, & Wurdack* 30483 (NY, US); shrub to 0.5 m., flowers white, fruit red, occasional in savanna, 1–I–1951, *Maguire, Cowan, & Wurdack* 30561 (NY, US); low sprawling shrub, leaves glaucous, fruit orange, 20–XI–1953, *Maguire, Wurdack, & Bunting* 36580 (holotype, US; isotype, NY).

3. *Humiria wurdackii* Cuatr., sp. nov.

PLATE 10

Frutex 1–3 m. altus ramulis tenuibus tortuosis griseis vel ultimis badiis, glaberrimis.

Folia coriacea glabra linearia, 2.5–10 cm. longa 3–8 cm. lata, apice angustata obtusa vel emarginata et mucronulata, mucrone 0.3–0.4 mm. longo calloso deciduo, basim versus ad modum petiolum subalatum 4–8 mm. longum angustata, margine integerrima eglandulosa vel prope margine parce subglanduloso-punctata, supra olivacea subnitida laevia tantum costa plana conspicua subtus pallide viridia costa

prominula nervulis minoribus laxe reticulatis paulo conspicuis vel obsoletis; saepe lamina secundum costam plicata.

Inflorescentiae axillares pauciflorae foliis breviores 1–3 ramis ad 15 mm. longis teneris glaberrimis. Bracteae crassiusculae ovatae obtusae amplexentae glabrae 0.5–0.7 mm. longae. Pedicelli 1–1.5 mm. longi crassi sursum ampliati. Sepala late rotundata circa 1.5 mm. longa inferne coalita crassa glabra margine minutissime ciliata excepto, eglandulosa vel raro glandula dorsale munita. Petala alba aestivatione cochlearia crassiuscula glabra linearia apice attenuata minuteque glanduloso-mucronulata, 5–7 mm. longa 1–1.3 mm. lata. Stamina 20 filamentis crassiusculis papillosis inaequilongis petala non attingentibus dimidia parte in tubum coalitis. Antherae circa 0.8 mm. longae connectivo crasso lanceolato acutiusculo thecis ellipsoideis basi breviter barbatis circa 0.4 mm. longis. Discus intrastaminalis annularis crassiusculus glaber 10-lobatus lobis emarginatis circa 1 mm. altus. Ovarium ovatum sursum pilosulum, circa 2 mm. altum, 5-loculare loculis biovulatis ovulis oblongo-ellipsoideis in loculo superpositis. Stylus erectus robustus hirtellus circa 3 mm. longus. Stigma 5-capitato-lobatum. Drupa ellipsoidea.

Type in the U.S. National Herbarium, No. 2282982, from Venezuela, Amazonas, Río Atabapo, 20 km. above San Fernando de Atabapo, abundant at margin of Sabana Cumare on right bank of Caño Cumare, elevation 125 m., collected June 3, 1959, by J. J. Wurdack and L.S. Adderley, No. 42760.

Shrub about 3 m. high with spreading, thin, glabrous branchlets. Leaves coriaceous, small, linear, entire, usually folded at length, obtusely narrowed and minutely mucronate at apex, narrowed into a subpetiole at base, 2.5–10 cm. long, 3–8 mm. broad, the midrib conspicuous above, prominent beneath, the veins inconspicuous above, loosely reticulate and slightly prominulous beneath.

Inflorescences short, axillary, usually with 5–10 flowers and 1–3 thin, glabrous branchlets up to 15 mm. long. Bracts ovate, obtuse, glabrous, 0.5–0.7 mm. long. Pedicels 1–1.5 mm. long, thickening towards the apex. Sepals broad, rounded, united at the lower half, 1.5 mm. long, glabrous except for the minutely ciliate margin, usually without glands, sometimes with a rounded gland on the back. Petals white, thick, glabrous, linear, attenuate at apex, ending with a minute callose gland, 5–7 mm. long, 1–1.3 mm. wide. Twenty stamens, little, shorter than the petals, united in the lower half forming a tube, the filaments rather thick, papillose, unequal in length. Anthers with a thick, lanceolate, acute connective, the thecae basal, ellipsoid, slightly hairy. Intrastaminal disk annular, about 10-lobate with emarginate lobes, 1 mm. high. Ovary hairy at the apex, 5-locular, each cell with

two superimposed ovules. Style erect, rigid, hairy, about 3 mm. long. Stigma capitate-lobate. Drupe ellipsoid.

H. wurdackii is characterized by its narrow, linear leaves, a unique feature in the family. This species has some relationship to *H. balsamifera* var. *laurina*. The species is only known from a single savanna in the Venezuelan Llanos, where it is abundant.

VENEZUELA, AMAZONAS: Río Atabapo, 20 km. above San Fernando de Atabapo, elev. 125 m., in Sabana Cumare, on right bank of Caño Cumare. Shrub 1–3 m., flowers white, locally abundant at margins of the Sabana, *J. J. Wurdack & L. S. Adderley* 42760.

4. *Humiria crassifolia* Mart. ex Urb. in Mart. Fl. Bras. 12(2):441. 1877.

FIGURES 21,u; 23,o,q-r; 25,a-b

Humirium crassifolium Mart. Nov. Gen. & Sp. Pl. 2:143–144, pl. 198. 1826.

Myriodendrum subvaginale Mart. ex Urb. in Mart. Fl. Bras. 12(2):441. 1877.

Type: *Martius*, Colombia, Caquetá, Sierra de Araracuara.

Small or medium-size tree with almost smooth, lustrous, glabrous, rather thick and densely leafy terminal branchlets. Leaves thick-coriaceous, rigid, glabrous. Petiole 1–2.5 cm. long, stout, winged, amplexant at base. Blade elliptic-ovate, little oblong, somewhat attenuate towards the base, slightly narrowed and obtuse or subrotundate at apex, entire and with some very distant gland-spots at margin; 7–16 cm. long, 4–9.5 cm. broad; above greenish, nitid, with

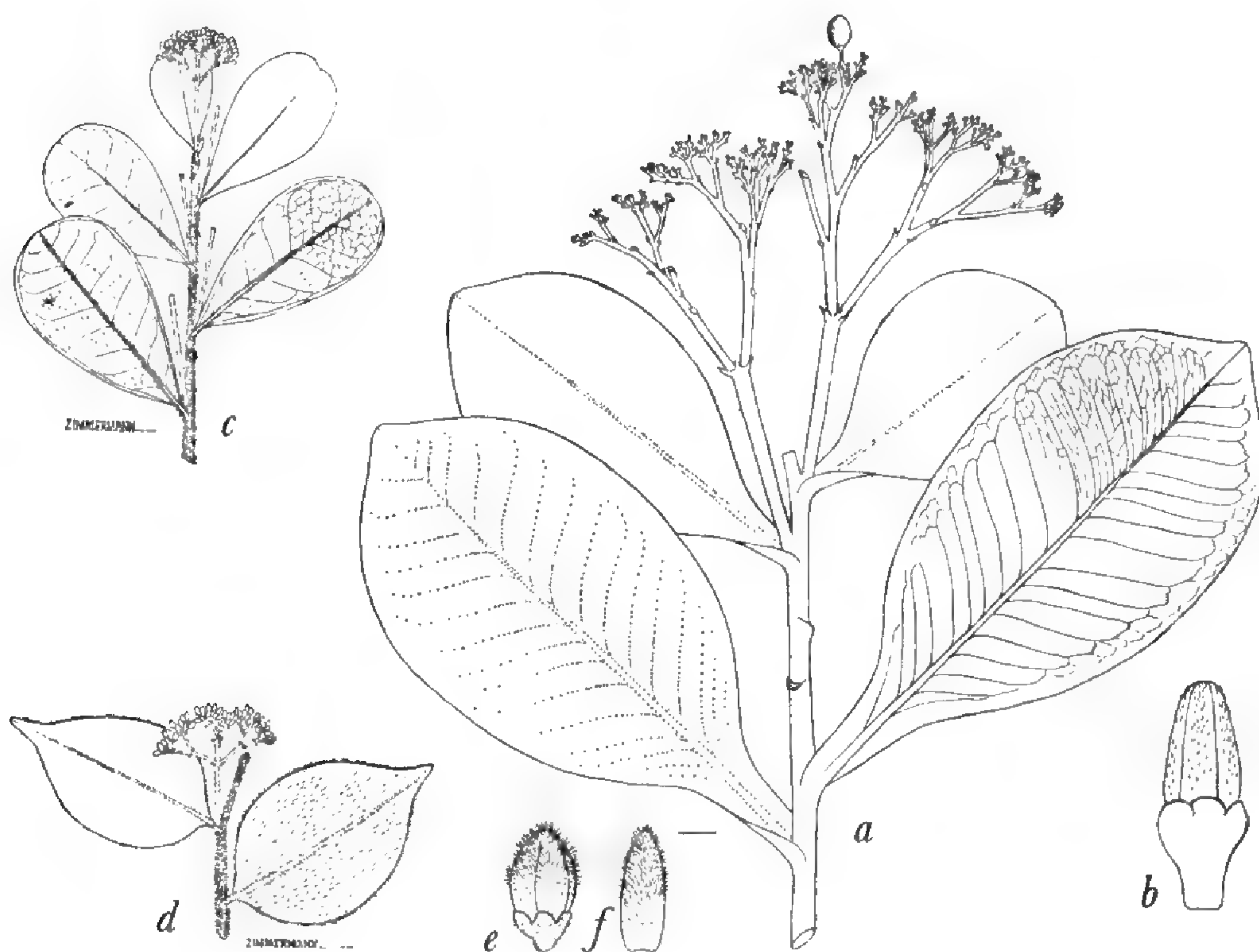


FIGURE 25.—a-b, *Humiria crassifolia*: a, $\times \frac{1}{2}$ (Maguire & Fenshawe 23233); b, bud, $\times 3\frac{1}{2}$ (Schultes & Cabrera 15054); c, *Humiriastrum obovatum*, $\times \frac{1}{2}$ (Gleason 729); d-f, *Humiriastrum villosum*: d, $\times \frac{1}{2}$ (Fróes 22644); e, bud, $\times 3\frac{1}{2}$; f, petal. $\times 3\frac{1}{2}$.

flat and broad midrib, lateral nerves obscurely prominulous, smaller obsolete; beneath with very thick midrib, 11–12 pairs of spreading secondary nerves slightly prominulous, near margin arcuate-anastomosate, minor veins parallel and reticulate, little conspicuous.

Inflorescences axillary-subterminal, cymose-paniculate, dichotomous, corymbiform, shorter than leaves; peduncle and branchlets compressed, glabrous. Bracts amplexant, persistent, ovate or triangular, acute, 2–1 mm. long. Fertile ultimate branchlets very short (0.5 mm. long), with bracteole 0.5 mm. long. Pedicels glabrous, thick, thicker towards apex, about 1 mm. long. Sepals rotundate, united at base, about 1 mm. long, minutely ciliate at margin, glabrous outside. Petals white, thick, rigid, linear-oblong, narrowed and subobtusate at apex, 5 mm. long, 1–1.5 mm. broad, puberulous outside. Stamens 20, filaments papillose, 4–5 mm. long, conerescent on lower half, 10 shorter alternating with longer ones. Anthers about 0.8 mm. long, thecae globose and hairy, connective ovate-lanceolate. Disk annular, scales linear, acute, united at base. Ovary globose, about 1 mm. high, glabrous, 5-locular, cells biovulate. Style rather thick, rigid, 3.5 mm. long, hirtellous. Stigmas 5, oblong-ellipsoid, translucent, connivent-stellate. Drupe ellipsoid, 10–12 mm. long, 7–9 mm. broad. Endocarp obovoid, subrounded at apex, subacute at base, 10–11 mm. long, 6.5–8 mm. broad, 5-foraminate at apex.

H. crassifolia is only known from the Cerro de Araracuara, Caquetá, Colombia (type locality), the Cerro Isibuquiri in Vaupés, and the Kaieteur Plateau in British Guiana. Probably it is spread further along the isolated mountains of the crystalline Guiana shield.

COLOMBIA: CAQUETÁ: "In sylva ad radicem montis Araracoara," *Martius* s.n. (holotype, M; isotypes, M). VAUPÉS: Río Cananarí, Cerro Isibuquiri, base de cuarcita, cerca del pico, 10 ft. tall, flowers white, yellow anthers, I-1952, *Schultes & Cabrera* 15054 (US).

BRITISH GUIANA: Kaieteur Plateau, from bush island in savanna, occasional; 6 m. tree, 12 cm. diam.; leaves rigid coriaceous; young fruit oval, green; seed bony pale brown; 5-V-1944, *Maguire & Fanshawe* 23233 (NY, US, U, VEN).

6. *Humiristrum*

Humiristrum (Urb) Cuatr., gen. nov.

Saccoglottis subgen. *Humiristrum* Urb. in Mart. Fl. Bras. 12(2):443. 1877.

Saccoglottis Sect. *Humiristrum* (Urb.) Reiche in Engl. & Prantl, Pflanzenfam. 3(4):37. 1890.

Sacoglottis Sect. *Humiristrum* (Urb.), Winkl. in Engl. & Harms, Pflanzenfam. 19a:128. 1931.

Humirium Benth. in Hook. London Journ. Bot. 2:373. 1843 (in part); in Hook. Journ. Bot. Kew Gard. Misc. 5:100. 1853.

Sepals 5, suborbicular, imbricate, united at base. Petals 5, free, thick-membranaceous, linear or oblong, the estivation quincuncial,

contorted, or cochlear. Stamens 20, in 2 alternating lengths, glabrous, filaments connate at base. Anthers ovate-lanceolate or oblong attached near base, thecae 2, unilocular, ellipsoid or subglobose, basal, connective thick, more or less lanceolate and acute at apex. Disk a dentate ring circling ovary or more or less free scales. Ovary 5-locular, cells uniovulate. Carpels opposite sepals. Ovules anatropous with ventral raphe, pendant at inner angles of ovary. Style short. Stigma capitate-lobate. Drupe medium-size or small, ellipsoid or subglobose, smooth, exocarp carnose, subcoriaceous when dry. Endocarp woody, usually without resinous cavities, 5 foramina (small holes) around apex and 5 oblong germinal opercula or valves on upper half. 1-2 seminiferous cavities well developed, rarely up to 5. Seeds oblong. Evergreen trees with coriaceous or subcoriaceous, simple, alternate, petiolate leaves, entire or dentate. Stipules small, deciduous or lacking. Inflorescences axillary or pseudoterminal, paniculate mostly with trichotomous or dichotomous branching. Bracts persistent or deciduous. (See also figs. 3, 26, and 29.)

Type species: *Humiriastrum cuspidatum* (Benth.) Cuatr.

"Humiriastrum" is a derivative name indicating resemblance to "Humiria."

Humiriastrum comprises 12 species spread throughout tropical South America from the eastern to the western coast going northward as far as Costa Rica and southward to Rio de Janeiro.

Key to the Species of *Humiriastrum*

1. Bracts persistent. Petals hispidulous, rarely glabrous. Ovary glabrous, rarely puberulous.
2. Leaves obovate-spatulate or elliptic-obovate, rounded or truncate at apex, attenuate at base, sessile or subsessile, margin revolute, pilose with hirsute midrib beneath, secondary nerves fine, spreading, prominent. Branchlets pubescent-hirsute **1. H. obovatum**
2. Leaves narrowed acuminate or cuspidate at apex, flat, nerves and veins obsolete or very little conspicuous, firmly coriaceous.
3. Leaf blades more or less villous-hirsute and densely so on midrib, ovate-acuminate or cuspidate. Terminal branchlets hirsute. Peduncle and branchlets of inflorescence hirsute, uppermost densely hirtellous. Sepals hirtellous **2. H. villosum**
3. Leaf blades glabrous. Terminal branchlets glabrous or rarely puberulous-hirtellous.
4. Drupe oblong-elliptic, 2.4-3 cm. long. Leaf blades ovate-oblong or elliptic-oblong, narrowed cuspidate. Petals hispidulous. Sepals shortly puberulous. Ovary sparsely puberulous or glabrous. **3. H. piraparanense**
4. Drupe globose, 1.7-2 cm. in diameter. Leaf blades ovate or elliptic-acuminate, abruptly cuspidate, more conspicuously dentate. Petals hispidulous or glabrous. Sepals glabrous outside. Ovary glabrous. **4. H. cuspidatum**

1. Bracts deciduous.

5. Inflorescence mostly terminal, as long or longer than the leaves, erect, corymbiform, multiflorous. Leaves glabrous above, sparsely covered with very minute, thin, appressed, inconspicuous hairs beneath; rather thick.
6. Young branchlets winged, glabrous. Leaves sessile or subsessile, broadly ovate or elliptic, rounded or obtuse at base, more or less amplexant. Ovary glabrous. Petals puberulous **12. H. procerum**
6. Young branchlets subterete or slightly angulate, pubescent or puberulous. Leaves short-petiolate, subobovate-elliptic or oblong-elliptic, cuneate at base. Ovary more or less pilose. Petals appressed pubescent or scarcely puberulous **11. H. diguense**
5. Inflorescences mostly axillary, shorter than leaves, usually divaricate-paniculate. Leaves completely glabrous or spreading-pilose.
7. Terminal branchlets hirsute or puberulous-hirtellous. Peduncles and branchlets of inflorescences hirsute or hirtellous.
8. Leaf blades softly spreading, pubescent or puberulous beneath, rigidulous, the midrib densely pubescent above, the secondary nerves and reticulum sharply prominulous on both sides. Branchlets very hirsute. Petioles 7-10 mm. long, hirtellous. Pedicels glabrous. Sepals glabrous outside **7. H. dentatum**
8. Leaf blades glabrous or inconspicuously puberulous, nervation inconspicuous above. Sepals minutely pilose outside. Pedicels pilose.
9. Petioles about 1 mm. long; leaf blades inconspicuously puberulous with minute, thin, subappressed hairs beneath; rigid coriaceous, secondary nerves slightly conspicuous, reticulum obsolete beneath. Petals hirtellous **9. H. subcrenatum**
9. Petioles 2-6 mm. long; leaf blades glabrous.
10. Petioles 2-3 mm. long. Leaf blades thin-coriaceous, flexible, rounded or obtusely cuneate at base, nerves and reticulum slightly prominulous beneath. Petals puberulous-hirtellous. Drupe ellipsoid-ovoid, $2-2.5 \times 1.4-1.8$ cm . . . **5. H. excelsum**
10. Petioles 3-6 mm. long. Leaf blades rigidulous-coriaceous, acutely cuneate at base, nerves and reticulum prominent beneath. Petals glabrous. Drupe globose, 1-5-1.6 cm. in diameter. **10. H. mapiriense**
7. Terminal branchlets glabrous. Leaves glabrous.
11. Leaves rounded at apex often abruptly, shortly and obtusely acuminate, abruptly and obtusely cuneate at base, subsessile, smooth above; with thick midrib, numerous thin spreading secondary nerves and prominulous reticulum beneath. Inflorescences terminal and subterminal, dichotomous, short-hirtellous-puberulous, becoming divaricate. Petals sparsely strigose. Drupe black, ovoid, apiculate, $1.6-1.8 \times 1-1.3$ cm **13. H. melanocarpum**
11. Leaves attenuate toward apex, acute, acuminate or cuspidate.
12. Petiole 6-11 mm. long. Leaf blades with midrib impressed above and prominent beneath, nerves and reticulum thin above, sharply prominent beneath. Peduncle and branchlets of inflorescence glabrous, rarely puberulous. Pedicels glabrous. Sepals glabrous outside. Petals glabrous. Ovary glabrous. Drupe ellipsoid-globose 1.9×2.2 cm **8. H. glaziovii**
12. Petiole 2-4 mm. long. Leaf blades smooth above, midrib prominulous, other nerves thin or inconspicuous beneath. Peduncle

and branchlets of inflorescence hirtellous. Pedicels puberulous. Sepals puberulous outside. Petals puberulous. Ovary hirtellous. Drupe ellipsoid-ovoid, $2-2.2 \times 1.2-1.5$ cm. **6. *H. colombianum***

1. *Humirium obovatum* (Benth.) Cuatr., comb. nov. FIGURE 25,c

Humirium obovatum Benth. in Hook. London Journ. Bot. 2:373. 1843.

Sacoglottis obovata (Benth.) Urb. in Mart. Fl. Bras. 12(2):443. 1877.

Type: *Schomburgk* 166, British Guiana.

Tree about 16 m. high with slender, grayish, pubescent-hirsute terminal branchlets. Leaf blades coriaceous, rigid, obovate or elliptic-obovate, more or less elongate, rounded or truncate-emarginate at apex or sometimes obtuse, attenuate toward base, cuneate-sessile or with very short winged petiole; margin apparently entire, strongly revolute; 2.5–9 cm. long, 1.4–4 cm. broad; green above, nitid, pubescent on midrib and margin, elsewhere glabrous, secondary nerves and veins scarcely conspicuous; hirtellous beneath with copious, thin, spreading hairs, midrib thick, hirsute, secondary nerves, 6–8 pairs, subprominent, patulous, near margin arcuate-anastomosate, veins prominent and lax-reticulate.

Inflorescences corymbose-paniculate, trichotomous or dichotomous, axillary in upper leaves, shorter than leaves, peduncle and branches pubescent-hirtellous. Bracts persistent, amplexant, triangular or ovate, acute, hirsute, 1–0.5 mm. long. Pedicels thick, hirsute, about 0.5 mm. long, articulate with 0.4–1 mm. long, thick, hirtellous peduncles. Sepals about 0.7 mm. long, hirtellous, connate at base, apex rotundate. Petals thick, oblong, subacute or subobtuse at apex, hirtellous, 2 mm. long, 0.8 mm. broad. Stamens about 20, filaments 0.8–1.2 mm. long, lower part connate. Anthers oblong, glabrous, about 0.6 mm. long, thecae subglobose, small, connective thick, sublanceolate. Disk annular, 0.4 mm. high, 20-denticulate, girdling ovary. Ovary subglobose, glabrous, 0.7–0.8 mm., 5-locular, cells uniovulate; ovules oblong, 0.4 mm. long. Style thick, about 0.6 mm. long. Stigma capitate, 5-lobate.

H. obovatum is a very well-defined species with a distribution limited to the British and Venezuelan Guianas.

BRITISH GUIANA: Upper Kamuni, 15–XII–1908, “hurihi,” collector ? (NY). Upper Kamuni River, “hurihi,” a low spreading savanna tree, bark used as an antiseptic, XII–1908, *Forest Department* (Anderson) 154 (K). Yam-pari Creek, 20 miles southwest of Georgetown, swampy land near stream on alluvial clay, flowers greenish, ripe fruit purplish black and eaten by parrots, medium-size tree not buttressed with smooth bark and reddish blaze, 29–V–1929, “hurihi,” (Arawak), *Forest Department* 931 (K). Sine loco, 1841, *Schomburgk* 166 (P, isotype). Sine loco, 1841, *Schomburgk* 135 (Richard) (M). Sine loco, 2nd expedition *Schomburgk* 825 (P). “Guiana Anglica,” *Schomburgk* 584 (NY). *Sylva ad lacunam* Tapacuma, VIII–1843, *Schomburgk* 1359 (GH, S, US, isoparatypes). Demerara River, 1887, “honronhi,” *Jenman* s.n. (NY, U). Butukari, dense upland forest, 20–21–VII–1921, *Gleason* 729 (GH, NY, US).

VENEZUELA: BOLÍVAR: Región de los ríos Icaború, Hacha y cordillera sin nombre a 280° de las cabeceras del Río Hacha, 450–850 m. alt.; selva pluvial o sabana natural; árbol 30 m., madera roja sin látex ni resina, hoja verde clara, flores en racimos abiertos, estambres numerosos erectos, 7–I–1956, *Bernardi* 2814 (NY).

2. *Humirastrum villosum* (Fróes) Cuatr., comb. nov.

FIGURE 25, *d–f*; PLATE 11

Sacoglottis villosa Fróes, Bol. Tec. Inst. Agr. do Norte 20:53. 1950.

Type: *Fróes* 22644, Brazil, Amazonas, Rio Padauri.

Medium-size tree with hirsute terminal branches. Leaves coriaceous, short-petiolate to subsessile. Blade ovate-acuminate or ovate-lanceolate, rotundate and abruptly and shortly cuneate at base, narrowed and acuminate at apex, margin slightly crenate or subentire; 3–6 cm. long, 2–3.8 cm. broad; above only prominent and hirsute midrib conspicuous, elsewhere almost smooth and glabrous; midrib prominent and hirsute beneath, remaining more or less densely and softly villous-hirtellous, minor nerves and veins immersed, obsolete.

Inflorescences axillary and subterminal, half the length of leaves, paniculate-cymose, lower branches trichotomous or dichotomous, peduncle 1–1.5 cm. long, straight, densely and spreadingly hirsute, branchlets densely hirtellous. Bracts persistent, ovate-oblong, hirtellous, 1.5–0.5 mm. long. Pedicels thick, 0.4–0.5 mm. long, hirtellous. Sepals 0.6 mm. long, ovate-orbicular, short-connate at base, hirtellous. Petals elliptic-oblong, subobtuse, hispidulous, about 3 mm. long and 1–1.3 mm. broad, estivation quincuncial. Stamens 20, the 2 sizes alternating, filaments complanate, about 1.2 and 1.6 mm. long, glabrous lower parts connate in a tube. Anthers 0.6–0.7 mm. long, thecae ellipsoid, connective carnose, ovate-acuminate. Disk formed by oblong, bitridentate, glabrous, scarcely adherent scales. Ovary globose, glabrous, 5-locular, cells uniovulate. Style 0.5 mm. long. Stigma shortly 5-lobate.

H. villosum is characterized by its general hirsute indument. The type specimens are densely hirsute, whereas Ducke's and Humbert's collections have a loose indument on leaves and branches; peduncles and calyx, however, are always abundantly hairy. This species is found in the upper Amazon Basin in the Rio Negro and Rio Vaupés regions, and it has also been collected far away in Obidos, in the State of Pará.

COLOMBIA: VAUPÉS: Río Cubiyú, afluente del Vaupés, 350 m. alt., 9–10–XI–1952, *Humbert & Schultes* 27363 (US, P).

BRAZIL: AMAZONAS: Cachoeira do Rio Araca, subafluente do Rio Negro, terra baixa; arvore de 7 metros, a beira do rio, flor branca, 29–X–1952, *Fróes & Addison* 29144 (IAN). Rio Negro, Paauiry, Rio Pitima, tree 50 ft., 16 in., greenish yellow flowers, on low land, high forest, border of river of blackish water, clay soil,

21-X-1947, *Fróes* 22644 (holotype IAN, isotype P). PARÁ: Obidos, campinas de areia ao sul da Serra do Valho-me Deus, 20-VII-1912, *Ducke* 12030 (MG).

3. *Humirastrum piraparanense* Cuatr., sp. nov.

FIGURE 26, e-g

Arbor parva vel media ramulis ultimis subteretibus glabris nitidis deinde griseis rugulosis. Folia coriacea breviter petiolata glabra. Petiolus 2-7 mm. longus crassiusculus complanatus anguste alatus. Lamina oblongo-ovata vel oblongo-elliptica basi subrotundata subite breviterque cuneato-angustata vel obtuse cuneata, apice longe

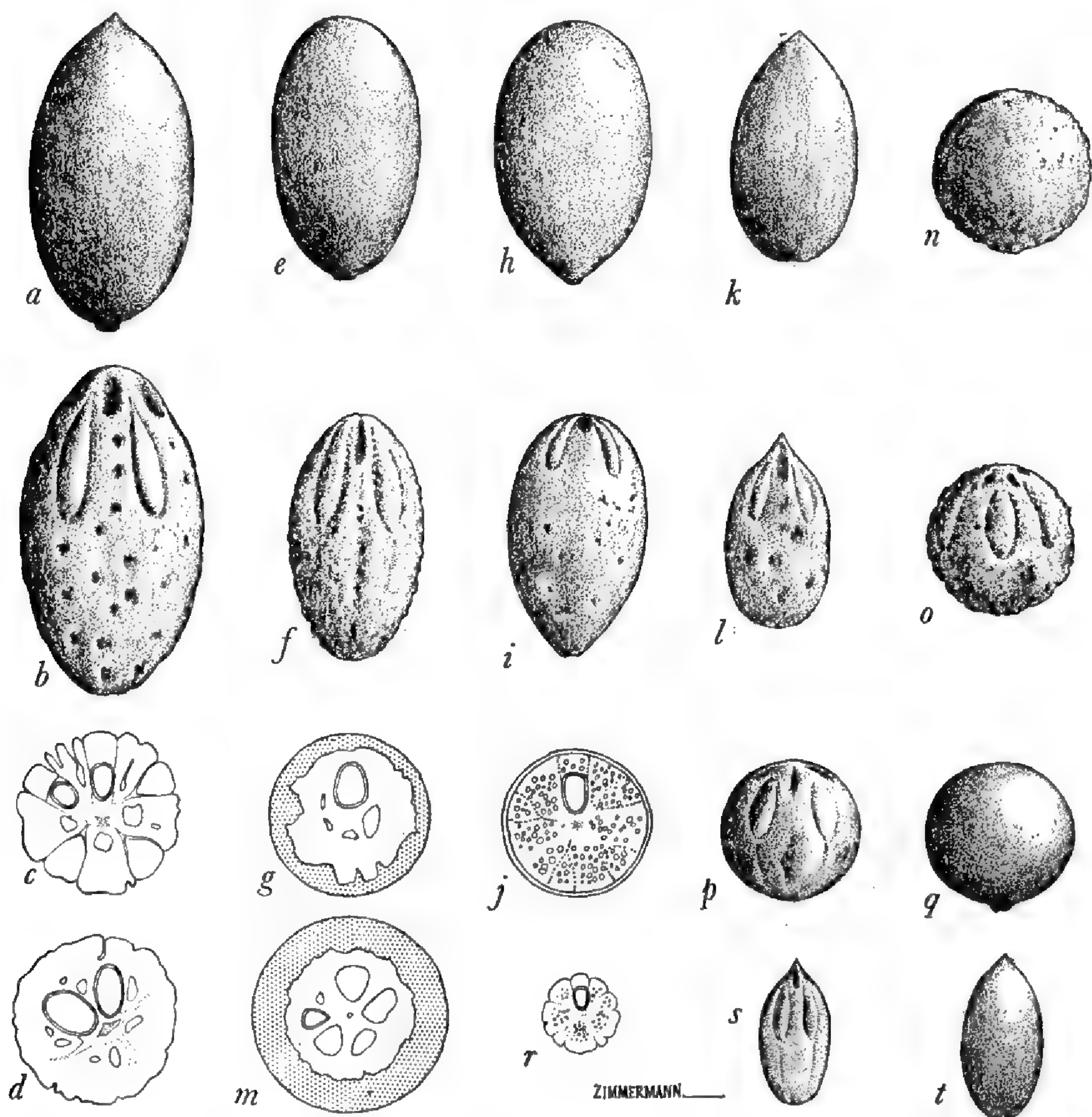


FIGURE 26.—*Humirastrum*, $\times 1$, fruit: a-d, *Humirastrum procerum* (Little 6320): a, fruit; b, endocarp; c, transection at upper third; d, transection at lower third. e-g, *Humirastrum piraparanense*, $\times 1$ (Schultes & Cabrera 15922): e, fruit; f, endocarp; g, transection. h-j, *Humirastrum excelsum*, $\times 1$ (Ducke 15459): h, fruit; i, endocarp; j, transection. k-l, *Humirastrum colombianum*, $\times 1$ (Romero Cast. 4942): k, fruit; l, endocarp. m, *Humirastrum cuspidatum*, $\times 1$ (Ducke 30126) transection. n-o, *Humirastrum cuspidatum* var. *glabriflorum*, $\times 1$ (Ducke 23436): n, fruit; o, endocarp. p-q, *Humirastrum mapiriense*, $\times 1$ (Krukoff 11270): p, endocarp; q, fruit. r-t, *Humirastrum melanocarpum*, $\times 1$ (Cuatrecasas 19909): r, transection; s, endocarp; t, fruit.

angustato-acuminata cuspidata, margine breviter vel obscure serrata plana, 7–13 cm. longa, 3–6 cm. lata, utrinque sublaevis subopaca costa crassa sed immersa vel subtus prominenti bene notata nervis secundariis 13–16 utroque latere valde tenuibus saepe inconspicuis prope marginem arcuato-anastomosatis, venulis minoribus tenuissimis reticulatis haud vel leviter visibilibus.

Inflorescentiae cymoso-paniculatae axillares foliis breviores pedunculo puberulo erecto plus minusve compresso apice trifurcato ramis trichotomis vel sursum dichotomo-ramosis, complanatis hirtulis; bracteis ovatis amplexantibus ciliolatis inferioribus 1 mm. longis sursum 0.5 mm., obtusiusculis vel subacutis, persistentibus. Flores plerumque ternati ad terminationem ramusculis ultimis hirtulis brevissimis usque 2 mm. longis. Pedicelli crassi brevissimi minute pubescentes, 0.2–0.3 mm. longi. Calyx ad 0.7–0.8 mm. altus sepalis basi coalitis, lobis rotundatis margine ciliolatis reliquis hispidulo-puberulis. Petala elliptico-oblonga obtusiuscula crassiuscula viridula extus pubescentia vel puberula circa 3 mm. longa 1.2 mm. lata aestivatione saepe contorta. Stamina 20 circa 2 mm. longa glabra filamentis crassiusculis complanatis minute papillosis, tertio inferiore coalitis 1.7 et 1.2 mm. longis parte libera directa integra acuta. Antherae circa 0.7 mm. longae glabrae thecis basalis minutis globosis vel transverse ellipsoideis connectivo crasso angulato multo longiori lanceolato. Discus in annulo circa 0.5 mm. alto margine acute 20-dentato ovarium cingens. Ovarium glabrum obovoideum circa 0.8 mm. altum apice subite in stylum 0.5 mm. longum attenuatum, 5-loculare, loculis uniovulatis. Stigma capitatum 5-lobatum. Drupa ellipsoidea vel ovato-ellipsoidea 2.4–3 cm. longa, 1.8–2.5 cm. diamitens, laevis nitida. Exocarpium circa 3 mm. crassum coriaceum in sicco granuloso-resinosum interiore parte magis fibrosum. Endocarpium lignosum eresinosum tuberculato-rugosum oblongo-ellipsoideum 2.2–2.6 cm. longum 1.4–1.7 cm. diamitenti, apice subacutatum, subapicem 5 foramina cum 5 operculis oblongis 7–11 mm. longis descendentes alternantia, 5 cavitatis seminiferis monospermis vel tantum 3–1 evolutis. Semina oblonga circa 1.5 cm. longa.

Type in U.S. National Herbarium No. 2279921, collected along the Río Piraparaná tributary of Río Apaporis in Comisaría del Vaupés, Colombia, March 9, 1952, by Richard Evans Schultes & Isidoro Cabrera (No. 15922), specimen with fruit; paratype in U.S. National Herbarium No. 2270077, collected in Loma Bucchia, 250–600 m. alt. at the Río Piraparaná, tributary of the Apaporis River, Comisaría del Vaupés, Colombia, August 28–31, 1952, by Hernando García Barriga (No. 14287), specimens with flowers.

Small or medium-size tree with terete, grayish, nitid, glabrous branchlets. Leaves coriaceous, rigid, rather thick, glabrous. Petiole

2–8 mm. long, rather thick, flattened above, narrowly winged on sides. Blade ovate-oblong, elliptic-oblong, sometimes ovate, subrotundate and abruptly short-cuneate at base, narrowed, acuminate, and cuspidate at apex, margin short-serrate and flat, 7–13 cm. long, 3–6 cm. broad, almost smooth on both sides, dull, midrib conspicuously broad, flat above, prominent below, secondary nerves 13–16 pairs, very slender and, as well as veins, immersed and inconspicuous.

Inflorescences cymose-paniculate, axillary, shorter than leaves, peduncle puberulous, erect, more or less compressed, trifurcate, branches trichotomous and above dichotomous, complanate, hirtellous. Bracts persistent, amplexant, ovate, obtuse, or subacute ciliate at margin, 1–0.5 mm. long. Pedicels thick, short, 0.2–0.3 mm. long, minutely pubescent. Flowers usually ternate on short (up to 2 mm.) hirtellous peduncles. Sepals 0.7–0.8 mm. long, connate at base, rounded, hispid-puberulous, margin ciliate. Petals rather thick, greenish, elliptic-oblong, subobtuse, about 3 mm. long, 1.2 mm. broad, pubescent or puberulous outside. Stamens 20, about 2 mm. long, the lower third connate, filaments thick, complanate acute, entire, longer ones about 1.7 mm. long, shorter ones 1.1–1.2 mm. long. Anthers about 0.7 mm. long, glabrous, minute thecae globose or ellipsoid, basal, connective thick, angular, lanceolate. Disk annular, 0.5 mm. high, acutely 20-denticulate, girdling ovary. Ovary about 0.8 mm. high, obovoid, glabrous or sparsely pilose, 5-locular, cells uniovulate. Style 0.5 mm. long. Stigma capitate 5-lobate. Drupe ellipsoid or ovate-ellipsoid, 2.4–3 cm. long, 1.8–2.5 cm. in diameter, smooth, lustrous. Exocarp about 3 mm. thick, coriaceous when dry, resinous-granulose becoming fibrous toward interior. Endocarp woody without resiniferous cavities, tuberculate-rugose, oblong-ellipsoid, 2.2–2.6 cm. long, 1.4–1.7 cm. in diameter, subacutish at apex, 5 foramina below apex alternating with 5 oblong, descending, 7–11 mm. long opercula; rarely 5 seminiferous cavities, usually only 3–1, monospermous, seeds oblong, about 1.5 mm. long.

H. piraparanense is very closely related to *H. cuspidatum*, from which it differs in its elongate, usually thicker, less markedly dentate leaves, its puberulous sepals and especially its larger oblong fruit. In the type specimen the ovary is puberulous.

COLOMBIA: VAUPÉS: Río Piraparaná, tributary of Río Apaporis, lower course, small tree, fruit yellow, 9–III–1952, *Schultes & Cabrera* 15922 (holotype). Río Piraparaná, Loma Buc-chía, 250–600 cm., alt., árbol 20 m., flores amarillas, 28–31–VIII–1952, *García Barriga* 14287 (paratype).

BRAZIL: AMAZONAS: Rio Vaupés, Panure caatinga, arvore pequena, flor branca, 15–XI–1947, *Pires* 1030 (IAN). Rio Içana, Estirão Santana, caatinga típica a margem do rio; arvore 15 m., 22–III–1952, *Fróes* 27985 (IAN); specimen with very good and typical fruit and leaves. Capoeira de Santana, solo arenoso; arvore 8 m. a margem do rio, 3–IV–1952, *Fróes* 28407 (IAN). Manaus,

beira do rio Tarumã, terra baixa; arvore de 4 m., flores branco-amareladas, 7-VIII-1949, *Fróes* 24924 (IAN).

4. **Humirium cuspidatum** (Benth.) Cuatr., nov. comb.

FIGURES 26,*m*; 27,*a-b*

Humirium cuspidatum Benth. in Hook. Journ Bot. Kew Misc. 5: 101. 1853.

Sacoglottis cuspidata (Benth.) Urb. in Mart. Fl. Bras. 12(2):444. 1877.—

Ducke, Arch. Jard. Bot. Rio Janeiro 3:178. 1922; 6:39. 1933.—Arch. Inst. Biol. Veget. Rio Janeiro 4:25, 29. 1937.

Sacoglottis excelsa var. *glabriflora* Ducke, ibid. 4:25. 1938.

Type: *Spruce* 1715 and 1915, Brazil, Amazonas, Barra de Rio Negro.

Medium-size tree with slightly rugose, lenticellate glabrous (in one variety hirtellous) terminal branchlets. Leaves rigid, coriaceous, glabrous. Petiole short, thick, broad, and flattened, 2–6 mm. long. Blade ovate-elliptic, elliptic or obovate-elliptic, cuneate at base tapering to the petiole, abruptly narrowed, acuminate or caudate at apex, serrulate-crenate at margin; 4–11 cm. long, 2–6 cm. broad; midrib broad and flat above, flat or prominent beneath, surface smooth on both sides lateral nerves immersed and inconspicuous.

Inflorescences axillary and subterminal, cymose-paniculate, shorter than leaves, peduncle robust, striolate more or less compressed, glabrous, (in one variety puberulous), 1–2.5 cm. long, branches trichotomous and (the superior) dichotomous, spreading, striolate, very sparsely hirtellous. Bracts ovate, subobtuse or subacute, glabrous, about 1 mm. long, persistent. Bracteoles ovate, puberulous, 0.8–0.4 mm. long, persistent. Pedicels very short, thick (0.2–0.4 mm. long). Sepals orbicular, connate at base, glabrous except for ciliate margin, about 0.6 mm. long. Petals rather thick, greenish, elliptic-oblong, subobtuse, 2.5–3 mm. long, 1.2–1.5 mm. broad, pubescent, puberulous or rarely glabrous. Stamens 20, filaments minutely papillose, lower third connate, ten 2–2.2 mm. long alternating with shorter about 1.7 mm. long. Anthers glabrous, 0.7–0.8 mm. long, connective thick, ovate-acuminate, thecae short-ellipsoid, basal. Disk formed by 0.5 mm. long ovate, deeply bidentate, more or less united scales. Ovary globose glabrous, 5-locular, cells uniovulate; ovules oblong, about 0.5 mm. long, pendent, with ventral raphe. Style 0.6 mm. long. Stigma capitate, 5-lobulate. Drupe globose, about 18–20 mm. diameter, exocarp thin and smooth; endocarp globose, rugose, about 17 mm. diameter, with 5 foramina at apex and 5 elliptic-oblong, 7 mm. long, descending opercula.

H. cuspidatum is a species of the upper central Amazonian Basin (Rio Negro, Vaupés, Manaos region), spreading to southern Venezuela



FIGURE 27.—*Humiriastrum*: a, *H. cuspidatum*, $\times \frac{1}{3}$ (Ducke 30126); b, *H. cuspidatum*, bud and petal, $\times 3\frac{1}{3}$ (Ducke 23434); c, *H. cuspidatum* var. *glabriflorum*, $\times \frac{1}{3}$ (Ducke 243); d, *H. cuspidatum* var. *glabriflorum*, petal and bud, $\times 3\frac{1}{3}$ (Ducke 23436); e, *H. colombianum*, $\times \frac{1}{3}$ (Lamb 141); f, *H. colombianum*, petal and bud, $\times 3\frac{1}{3}$ (Lamb 141); g, *H. excelsum*, $\times \frac{1}{3}$ (Ducke 1614); h, *H. excelsum*, petal and bud, $\times 3\frac{1}{3}$ (Ducke 1614); i, *H. glaziovii* var. *glaziovii*, $\times \frac{1}{3}$ (Ducke 19166); j, *H. glaziovii* var. *glaziovii*, bud and petal, $\times 3\frac{1}{3}$ (Ducke 19166); k, *H. glaziovii* var. *angustifolium*, leaf, $\times \frac{1}{3}$ (Glaziov 16724); l, *H. dentatum*, $\times \frac{1}{3}$ (Glaziov 18178); m, *H. dentatum*, bud and petal, $\times 3\frac{1}{3}$ (Glaziov 18178).

and to the State of Pará. It grows mostly in inundated places but, especially its varieties, can also be found on elevated ground. According to Ducke (p. 25, 1938), it is frequent in central parts of Amazonia along the sandy river banks periodically flooded, the lakes, swamps, and still-water rivers that are poor in sediments. The mature drupe (according to Ducke) is globose, 15–25 cm. in diameter, black purplish with thin, juicy, red mesocarp, which has an astringent taste; when dry it is black and lustrous.

Key to the Varieties of *Humiriastrum cuspidatum*

1. Young branchlets glabrous. Peduncle of inflorescence glabrous.
 2. Petals hispidulous 4a. var. *cuspidatum*
 2. Petals glabrous 4b. var. *glabriflorum*
1. Young branchlets pubescent-hirtellous. Peduncle of inflorescence minutely puberulous. Petals glabrous or subglabrous . . . 4c. var. *subhirtellum*

4a. *Humiriastrum cuspidatum* var. *cuspidatum*.

VENEZUELA: BOLÍVAR: Piedra Marimare, east Bank of Río Orinoco opposite head of Isla El Gallo, tree 18 m., young fruit green, morichal, edge at east base of Piedra, 2 km. east of river, alt. 100 m., 20-XII-1955, *Wurdack & Monachino* 40881 (US).

BRAZIL: PARÁ: Campina entre as Serras do Dedale da Igaçaba, 4-IX-1907, *Ducke* 8628 (BM, MG). Baixo Yamunda, Lago das dois bocas, beira do campo alagado, 18-V-1911, *Ducke* 11790 (BM, MG). Rio Jamundá; praia Porto Rico, Municipio de Faro; arvore, fruto verde, "uchirana," "achua," 15-XI-1950, *Black & Ledoux* 50-10783 (IAN, US). AMAZONAS: Prope Panure ad Rio Vaupxès, X-1852-I-1853, *Spruce* 2424 (K, NY, S, P); 2443 (GH, K, P). Rio Negro prope Barra, VII-1851, *Spruce* 1715 (isotypes, US, GH, P, NY); 1915 (K, holotype "Herbarium Hookerianum"; M, isotype), photo F.M. 12593. Rio Curicuriary, afluyente Rio Negro ad ripas inundabilis; arbor parva vel mediocris, floribus viridibus, fructus violascenti-nigris, 4-X-1935 (fl.), 26-II-1936 (fr.), *Ducke* 30126 (US, S, U); *Ducke* s.n. (IAN). Rio Curicuriary (middle course), small tree, I-1948, *Schultes & López* 9701 (US). Rio Apurahu inferior afluyente Rio Negro, silva inundabili; arbor media, floribus viridibus odoratis, 26-VII-1929, *Ducke* 23434 (US). Rio Urubu, Sucuriju, terra firme baixa; arvore 7 m., flores esbranquiçadas, 29-IX-1949, *Fróes* 25438 (IAN). Without locality, *Schultes* 23131 (IAN). Without locality, *Martius* s.n. (P).

4b. *Humiriastrum cuspidatum* var. *glabriflorum* (Ducke) Cuatr., comb. nov.

FIGURES 26,n-o; 27,c-d

Sacoglottis excelsa var. *glabriflora* Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 4:25. 1938.

Type: *Ducke* 23436, Brazil, Amazonas, Manaus.

Ramuli hornotini glabri. Pedunculi inflorescentiae et rami majores glabri, superiores hirtulo-puberuli. Petala glabra.

This variety differs from *cuspidatum* in its glabrous petals and the usually smaller leaves. All other characters, including the globose fruit, completely agree with the available collections of *cuspidatum*.

BRAZIL: AMAZONAS: Manaus, prope Cachoeira do Mindú, silva non inundabilis, solo arenoso humoso; arbor magna floribus viridibus odoratis, "achuá," 22-VII-1936, *Ducke* 243 (A, NY, S, US); 8-VII-29, *Ducke* 23436 (US, P, S, U, isotypes). Manaus, Cachoeira Alta do Tarumá, terra umida, arvore de 8 m., flor amarela, 11-VIII-1945, *INPA* 204 (MG. 21546). Manaus, margem do Igarapé de Forquilha; arvore de copa densa e baixa, flor esverdeada com o centro castanho, 22-VIII-1955, *INPA* 1700 (MG 21542). São Paulo de Olivença, terra firme alta, arvore, IV-1945, *Fróes* 20803 (IAN, K, NY).

4c. *Humiriastrum cuspidatum* var. *subhirtellum* Cuatr., var. nov.

Ramuli hornotini hirtuli-pubescenti vel hirtuli-puberuli. Pedunculi ramique inflorescentiae minute puberuli. Petala glabra vel subglabra.

Type in the Herbarium of Instituto Agronómico do Norte, Belém do Pará, Brazil, collected on the margin of Rio Urubú, near São Francisco in the State of Amazonas, Brazil, October 4, 1949, by R. Lemos Fróes (No. 25480).

This variety has an uncertain position. The very young fruit are more or less oblong and their final form is unknown. The leaf characters agree very much with those of *H. cuspidatum* and its variety *glabriflorum*.

BRAZIL: AMAZONAS: Rio Urubú, São Francisco, beira do rio, arvore de 5 m., Fróes 25480 (IAN, holotype). São Francisco, 24-VIII-1949, Fróes 24820 (IAN). São Francisco, tierra firme baixa, arvore 8 m., 3-X-1949, Fróes 25463 (IAN).

5. *Humiriastrum excelsum* (Ducke) Cuatr., comb. nov.

FIGURES 26, *h-j*; 27, *g-h*

Sacoglottis excelsa Ducke, Arch. Bot. Rio Janeiro 3:178. 1922; 5:143, pl. 14 fig. 41. 1930; 6:39. 1933.—Arch. Inst. Biol. Veget. Rio Janeiro 4:25, 29. 1937.

Type: *Ducke* 15459, Brazil, Pará, Belém.

Large tree with pubescent-hirtellous or puberulous branchlets. Leaves thin-coriaceous, flexible, glabrous. Petiole 2–3 mm. long, puberulous beneath or glabrous. Blade ovate or ovate-elliptic, broadly cuneate or subrounded at base, more or less abruptly narrowed, acuminate or cuspidate at apex, flat and slightly crenulate-serrate at margin; 2.5–9 cm. long, 1.5–5 cm. broad; above with flat midrib, slender secondary nerves and veins almost obsolete; beneath midrib prominent, filiform secondary nerves, 10–12 pairs, prominulous, subpatulous, near margin reticulate-anastomosate, reticulum prominulous.

Inflorescence axillary, short, cymose-paniculate, mostly trichotomous, upwardly dichotomous, peduncle and branchlets minutely pubescent-hirtellous. Bracts minute, early deciduous. Pedicels rather thick, pubescent 0.2–0.4 mm. long, articulate with short and minutely pubescent peduncles. Sepals 0.6–0.8 mm. long, rotundate, minutely pubescent, margin ciliolate. Petals linear-oblong, attenuate at apex, subacute, hirtellous-puberulous, about 2.5 mm. long, 1 mm. broad. Stamens 20, filaments connate at base, about 1.5 mm. long, more or less papillose. Anthers about 0.8 mm. long, thecae ellipsoid a third or a fourth of total length, connective lanceolate, acute. Disk annular, 0.3–0.4 mm. high, dentate. Ovary ovoid, glabrous, 5-locular, 5-ovulate. Style 0.6 mm. long. Stigma capitate, 5-lobate. Drupe ellipsoid-ovoid, 2–2.5 cm. long, 1.4–1.8 cm. broad; exocarp smooth; endocarp woody with 5 foramina at apex and 5 oblong opercula, about 6 mm. long around apex.

H. excelsum is a large tree of the uninundatable forests of the Amazon basin. It is frequent in the Belém region (Pará) and is also reported from French Guiana and eastern Peru. The fruit are more or less oblong and yellowish with oleagineous mesocarp, and sweet and fragrant when ripe. The tree, according to Ducke, attains a height of 45 m. and has a brownish-red bark.

FRENCH GUIANA: Rivière "la Compté" rive droite à 50 m. en amont du Saut-Bief chemin minier de Bief et à 3 km. 500 de la rive Montagne Papillon; sur le flanc d'une montagne, pente raide; sol argileux; "prefontaine," 29-I-1957, *Bena* 1319 (U).

BRAZIL: PARÁ: Santa Izabel (Belém-Bragança) grand arbre de la forêt, "achuá," 18-IX-1908, *Museu Goeldi* 9672 (MG, US). Belém, silva non inundabilis; arbor magna vel maxime floribus viridibus odoratus, "achuá-rana," 16-IX-1922, *Ducke* 17780 (NY, P, S, US, U), photo F.M. 12597. Belém, grand arbre de la forêt, "achuá," 20-VIII-1914, *Ducke* 15459 (isotypes, MG, US). Belém, Catu, mata da terra firme, arvore grande, flor verde, 31-VIII-1944, "achuá," *Ducke* 1614 (A, IAN, MG, NY, US). Beira do rio Mapua, entre Vila Emilia e Boca do Mapua, varzea; arvore com folhas pequenas, 18-VII-1950, *Black, Fróes, & Ledoux* 50-9811 (US, IAN).

PERU: HUÁNUCO: Tingo Maria, Lote Dianderas (carretera Huánuco-Pucallpa) 800-900 m.; suelo arcilloso, pendiente mediana, selva lluviosa; árbol 20-30 m., 40-60 cm. diam., madera dura, de construccion, corteza rojiza, descamándose superficialmente, albura clara, duramen rojizo oscuro; relativamente abundante, "quinilla," 18-VII-1946, *Burgos* 85 (Y). Tingo Maria, a 1-2 km. carretera Huánuco-Pucallpa, km. 160, 800 m. alt., suelo arcilloso, profundidad mediana; selva densa; árbol 30 m., 60-100 cm. diámetro, flores amarillentas, olorosas; madera dura, rojiza, usada en postes, durmientes, columnas, etc. Crecen en grupos ± densos y se destacan por su color canela; la corteza se desprende sola en árboles viejos; regularmente abundante, "hispi," 28-VIII-1945, *Burgos* 37 (Y).

6. *Humiriastrum colombianum* (Cuatr.) Cuatr., status nov.

FIGURES 26,k-l; 27,e-f

Sacoglottis excelsa var. *colombiana* Cuatr., *Brittonia* 8:196. 1956.

Type: *Lamb* 141, Columbia, Santander, Cimitarra.

Medium-size or large tree, trunk with reddish brown, smooth bark and reddish, very hard wood. Terminal branchlets slender, brownish, glabrous. Leaves thin-coriaceous, glabrous. Petiole 2-4 mm. long, rounded and thickened at base. Blade elliptic or ovate-elliptic, abruptly cuneate and tapering to petiole at base, abruptly narrowed and acutely cuspidate at apex, margin crenulate; 4-7 cm. long (including tail), 1.5-3.5 cm. broad; above green with prominulous and conspicuous midrib, other nerves immersed, visible or obsolete; beneath lightly brownish with prominent and very conspicuous midrib, secondary nerves, about 9 pairs, extremely thin, near margin reticulate-anastomosate, very slightly prominulous or obsolete, veins obsolete.

Inflorescence cymose-paniculate, axillary and subterminal, shorter than leaves, lower branching trichotomous, superior dichotomous, peduncle 1-1.5 cm. long, rigid, striolate, slightly puberulous, branch-

lets articulate, more or less spreading hirtellous-puberulous. Bracts deciduous. Bracteoles ovate, 0.2–0.3 mm. long, puberulous, soon deciduous. Pedicels very short, thickened, puberulous, 0.2 mm. long; flowers practically sessile. Sepals 0.4–0.5 mm. long, rounded, minutely papillose, puberulous, ciliolate. Petals oblong, 2–2.1 mm. long, about 1 mm. wide, subappressed-puberulous. Stamens 20, filaments more or less papillose, 10 about 1.1–1.2 mm. long, alternating with 10 shorter ones about 0.7–0.8 mm. long. Anthers oblong-lanceolate, 0.7–0.8 mm. long, thecae short-ellipsoid, basal, connective thick-lanceolate. Several small, subdentate, 0.2 mm. long 0.1–0.2 mm. broad, free scales circling ovary and forming disk. Ovary globose, hispidulous, 5-locular, cells uniovulate. Style about 0.5 mm. long. Stigma capitate, 5-lobulate. Drupe ellipsoid-ovoid, rounded at base, abruptly narrowed and subacute or acute at apex, 20–22.5 mm. long, 12–15 mm. broad; exocarp glabrous, smooth thin (0.5 mm.) when dry; endocarp ovoid-ellipsoid, rounded or subtruncate at base, acutely acuminate at apex, woody, hard, rugose, barely pentagonal with 5 apical foramina and 5 subapical oblong, 6 mm. long, descending opercula.

H. colombianum differs from the Amazonian *H. excelsum* in its somewhat smaller leaves, which are attenuate and longer cuneate at the base and much longer cuspidate at the apex (the caudex is very acute, 1–1.5 cm. long, the nervation on the leaves is almost obsolete), in the glabrous young branchlets, in the free scales of the disk, and in the hispidulous ovary.

COLOMBIA: SANTANDER: Región del Carare (valle del Magdalena), Cimitarra, km. 3 camino del Ermitaño, tree 20 in. diameter, 60 ft. tall, forest canopy, "aceituno," 29–VII–1954, *Lamb* 141 (holotypus, US); 30–VII–1954, *Lamb* 145 (COL, US); forest tree 25 in. diameter, 50 ft. tall top canopy; wood hard, pink when fresh; "aceituno"; 17–VIII–1954, *Lamb* 170 (COL, US). Barranca Bermeja, 12 leguas al sureste, a 5 km. de la margen derecha del río Opón, 200 m. alt.; árbol 20 m., madera rojiza, dura, pesada, para polines y pilotes, corteza rojiza un tanto áspera, aletas basales cortas, ramillas parduscas, "aceituno," 28–IX–1954, *Romero Castañeda* 4942 (COL, US). Diez leguas al SE de Barranca Bermeja, 8 km. de la margen izquierda del río Opón; árbol 25 m., corteza gris, lisa, pardo rojiza, manchada de gris, albura rosada, corazón rojo, ramillas parduscas, madera dura para formaleas y entablados, \pm 200 m., "aceituno," 31–VIII–1954, *Romero Castañeda* 4785 (COL, US).

H. colombianum is only known from the Magdalena Valley in Colombia, where it is called "aceituno." Up to now it is also the only recorded species of the genus from the interior valleys of Colombia. *H. colombianum* is a large buttressed tree, the hardwood of which may be used in construction work; it is frequent in the rain forest on elevated ground.

7. *Humirium dentatum* (Casar.) Cuatr., comb. nov. FIGURE 27, l-m

Humirium dentatum Casar. Nov. Stirp. Bras. Decas IV: 38. 1842.—Benth. in Hook. Journ. Bot. Kew Misc. 5:102. 1853.

Sacoglottis dentata Urb. in Mart. Fl. Bras. 12(2):444 (in part). 1877.—Ducke, Arch. Jard. Bot. Rio Janeiro 5:143, pl. 14, fig. 40. 1930.

Type: *G. Casaretto*, Brazil, "from the sandy maritime woods called restingas in the Province of Rio de Janeiro."

Tree with pubescent-hirsute terminal branchlets. Leaves coriaceous, subrigid. Petiole 7–10 mm. long, narrowly winged, pubescent-hirtellous. Blade ovate or elliptic-lanceolate, more or less oblong, narrowed and obtusely short-cuneate at base, attenuate and acuminate at apex, margin serrate-dentate, slightly revolute, 4–11 cm. long, 1.5–5 cm. broad; above with minutely and densely pubescent midrib, elsewhere glabrous, secondary nerves filiform, veins forming a conspicuous, more or less prominulous reticulum; beneath softly and sparsely pubescent, prominent striolate midrib, subdensely hirtellous, prominulous secondary nerves about 10 pairs, subascendent, curvate-anastomosate near margin, veins reticulate and prominulous.

Inflorescence cymose-paniculate, axillary, shorter than leaves, dichotomous, peduncle and branchlets densely hirtellous. Bracts deciduous, ovate-oblong, subobtuse, puberulous, 1–0.5 mm. long. Pedicels thick, glabrous, 0.5–0.8 mm. long, articulate with glabrous or glabrescent, 0.5–2 mm. long peduncles. Sepals orbicular, connate at base, glabrous except ciliate margin. Petals rather thick, oblong, subobtuse, glabrous, about 2.5 mm. long, 1 mm. broad. Stamens 20, filaments 2–2.5 mm. long, connate at lower third, glabrous. Anthers glabrous, oblong-lanceolate, connective thick, thecae basal and oblong. Disk membranaceous, about 0.6 mm. high, short-dentate, girdling ovary. Ovary ovoid, glabrous, 1 mm. high, 5-locular with uniovulate cells, ovules elliptic-oblong, about 0.8 mm. long. Style robust, 0.5–0.6 mm. long. Immature fruit obovate.

Urban included in his "Flora Brasiliensis" a hirtellous and a glabrous form in the description of *Sacoglottis dentata*. The hairy plants undoubtedly belong to this species and agree with the original description by Casaretto. Urban saw in glabrous plants an unnamed variety which, I believe, is the species described later by Urban as *Sacoglottis glaziovii*. I have seen no authentic material of *H. dentatum*, but it is possible that specimens in Paris without the collector's name (from the Drake or Richard Herbaria) belong to the Casaretto collections.

At present *H. dentatum* is known only from the Rio de Janeiro region.

BRAZIL: RIO DE JANEIRO, *Glaziou* 18178 (NY, P), photo F.M. 12595. "Herb. Richard, *Humirium dentatum* Casar. Bresil F. Nob. 1855" (P). Rio de Janeiro,

1851, *Anderson* s.n. (S). SÃO PAULO: Santos, Sorocaba, I-1875, *Mosén* 3475 (P, S). "Herb. E. Drake, *Humirium dentatum* Casar." (P)

8. *Humirastrum glaziovii* (Urban) Cuatr., comb. nov. FIGURE 27,i-j

Sacoglottis dentata var. Urb. in Mart. Fl. Bras. 12(2):445. 1877.

Sacoglottis glaziovii Urb. Bot. Jahrb. Engler 17:503. 1893.

Type: *Glaziou* 18964, Brazil, Rio de Janeiro, Nova Friburgo, Alto Macahé; photo of holotype in Berlin-Dahlem, F.M. 12598.

Small or medium-size tree with glabrous, greenish and nitid young branchlets becoming rugose, brownish, and lenticellate. Leaves coriaceous, subrigid, glabrous. Petiole 6–11 mm. long. Blade elliptic-ovate or ovate-lanceolate, obtuse or short-cuneate at base, abruptly acuminate at apex, the margin serrate-dentate, flat or slightly revolute, 3.5–10 cm. long, 1.5–5 cm. broad; above nitid with impressed and thin midrib, lateral nerves and reticulum little prominent but conspicuous; beneath with prominent midrib, 9–10 pairs of filiform secondary nerves prominulous, subascendent, anastomosate near the margin, minute reticulum prominent.

Inflorescences cymose-paniculate, axillary, much shorter than leaves. Peduncle and dichotomous (rarely trichotomous) branches glabrous or smaller branchlets hirtellous-puberulous. Pedicels short (0.2–0.3 mm.), glabrous, articulate with 0.4–2 mm. long glabrous peduncle. Sepals about 1 mm. long, rotundate, glabrous except the minutely ciliate margin. Petals oblong, rather obtuse and thick, glabrous, 3–3.5 mm. long, 1 mm. broad. Stamens 20, with 2.5–3 mm. long filaments, glabrous and connate at base. Anthers glabrous, ovate-lanceolate, thecae oblong and as long as a half to a third of the acute connective. Disk annular, membranous, girdling ovary, deeply dentate, 0.6–0.7 mm. high. Ovary ovoid, glabrous, about 8 mm. high, 5-locular with uniovulate cells. Style about 0.7 mm. long. Stigma capitate. Drupe ellipsoid-globose, smooth, glabrous, about 19×22 mm. in diameter.

The concept of *H. glaziovii* includes the glabrous variety of *S. dentata* mentioned by Urban: "Var. ramulis, foliis, inflorescentiis glaberrimis." *H. glaziovii* grows in "restinga" type forests and secondary woods of the Rio de Janeiro region.

8a. *Humirastrum glaziovii* var. *glaziovii*. FIGURE 27,i-j

BRAZIL: RIO DE JANEIRO: Restinga de Maná, 30-XI-1896, avec Mr. Schwacke, *Glaziou* 18179 (NY, P, US); *Glaziou* 18964, photo F.M. 12598. Porto da Estrella, silvestris siccioribus; arbor parva, floribus viridibus inodris, in silvula secundaria sicciora, 17-XI-1925, *Ducke* 19166 (P, S, U, US). "Brasilia, *Humiria dentata* Cassaretto, *Sacoglottis*, Ex herbario horti Petropolitani," *Riedel* s.n. (P, K).

8b. *Humiriastrum glaziovii* var. *angustifolium* Cuatr., var. nov.FIGURE 27,*k*

Lamina folii anguste lanceolata basi cuneata crassior coriacea, 2.7–6.5 cm. longa 1–2 cm. lata.

Type in the U.S. National Herbarium, No. 1123930, collected at Alto Macahe, State of Rio de Janeiro, Brazil, February 6, 1888, by M. A. Glaziou (No. 16724). Isotypes at the U.S. National Herbarium, Nos. 483735 and 287412, in the Kew Herbarium and in the Herbarium of the Arnold Arboretum.

This variety differs from the typical form only in its narrower, lanceolate, and firmer leaves. It is only known from the Rio de Janeiro region and São Paulo in Brazil.

BRAZIL: SÃO PAULO: Arvore da Matta da Estação Biologica, 5–III–1919, *Hoehne* 3021 (NY). RIO DE JANEIRO: Prov. Nov. Friburgo, Alto Macahé, 6–II–1888, *Glaziou* 16724 (type US, K, A).

9. *Humiriastrum subcrenatum* (Bentham) Cuatr.

PLATE 12

Humirium subcrenatum Benth in Hook. London Journ. Bot. 2:374. 1843.—
Hook. Journ. Bot. Kew Misc. 5:102. 1853.

Humiria subcrenata Urb. in Mart. Fl. Bras. 12(2):442. 1877.

Sacoglottis subcrenata Urb. Sitz. B. Ges. Naturf. Berl. 5. 1878.

Type: *Martin*, French Guiana, Cayenne.

Terminal branchlets hirtellous. Leaves rigid coriaceous subsessile; petiole about 1 mm. long hirtellous; blade subelliptic shortly and obtusely acuminate at apex, cuneate at base, subentire or slightly crenate except toward the base, 2.6–4.5 cm. long, 1.7–2.8 cm. broad; above lustrous, glabrous or with minute hairs on conspicuous midrib, veins obsolete; below inconspicuously puberulous by minute, sparse hairs, midrib prominent, 8–10 pairs of secondary nerves extremely thin or inconspicuous, minor veins obsolete.

Inflorescences axillary shorter than leaves, cymose-paniculate, subdichotomous, above branchlets alternate, peduncle 9–12 mm. long, branchlets angulate and hirtellous; the pedicels 0.2–0.4 mm. long, hirtellous; bracts and bracteoles soon deciduous; calyx about 0.8 mm. high, quincuncial; sepals free, truncate-rounded, minutely ciliate at margin and minutely puberulous outside, 0.5 mm. high, 0.8 mm. wide. Petals thickish, linear, acute, hirtellous outside, 2.1–2.3 mm. long, 0.6 mm. broad. Stamens 20, glabrous, filaments united near base, 2 lengths, 1.1 and 1.4 mm., alternating; anthers thick, acute, about 0.6 mm. long, thecae minute basal, 0.15 mm. broad. Disk cupular, 0.7 mm. high, 20-denticulate. Ovary ellipsoid, appressed from top, minutely hirtellous, 5-loculate, cells uniovulate, ovules deltoid acute at apex. Style thickish, glabrous, 0.7 mm. long.

H. subcrenatum is only known from the type specimen from French Guiana. Urban treated this as “species dubia” under *Humiria*, but

in the following year (1878), after seeing original material sent to him by Bentham and Oliver, he published the right identification of the species as *Sacoglottis subcrenata* in the section *Humiriastrum*.

FRENCH GUIANA: Cayenne, *Martin* s.n., Herbarium Hookerianum, holotype (K).

10. *Humiriastrum mapiriense* Cuatr., sp. nov.

FIGURES 26,p-q; 28,g; PLATE 13

Arbor media ramis terminalibus griseis tenuibus minute puberulo-hirtulis.

Folia parva coriacea petiolo crassiusculo puberulo 3–6 mm. longo. Lamina obovata vel rhomboideo-obovata vel oblanceolata basi valde cuneata in petiolum attenuata apice angustata acutiuscule acuminata, margine serrato-crenulata, utrinque glabra; 3–4 cm. longa 1.5–2.5 cm. lata supra costa plana visibili ceteris nervis vix obsoletis; subtus costa elevata nervis secundariis filiformibus 8–9 utroque latere paulo adscendentibus arcuato-anastomosatis, nervulis venulisque prominulis reticulatis.

Inflorescentiae axillares et subterminales cymoso-paniculatae folia excedentes dichotomae vel inferne trichotomae pedunculo 1.5–2.5 cm.

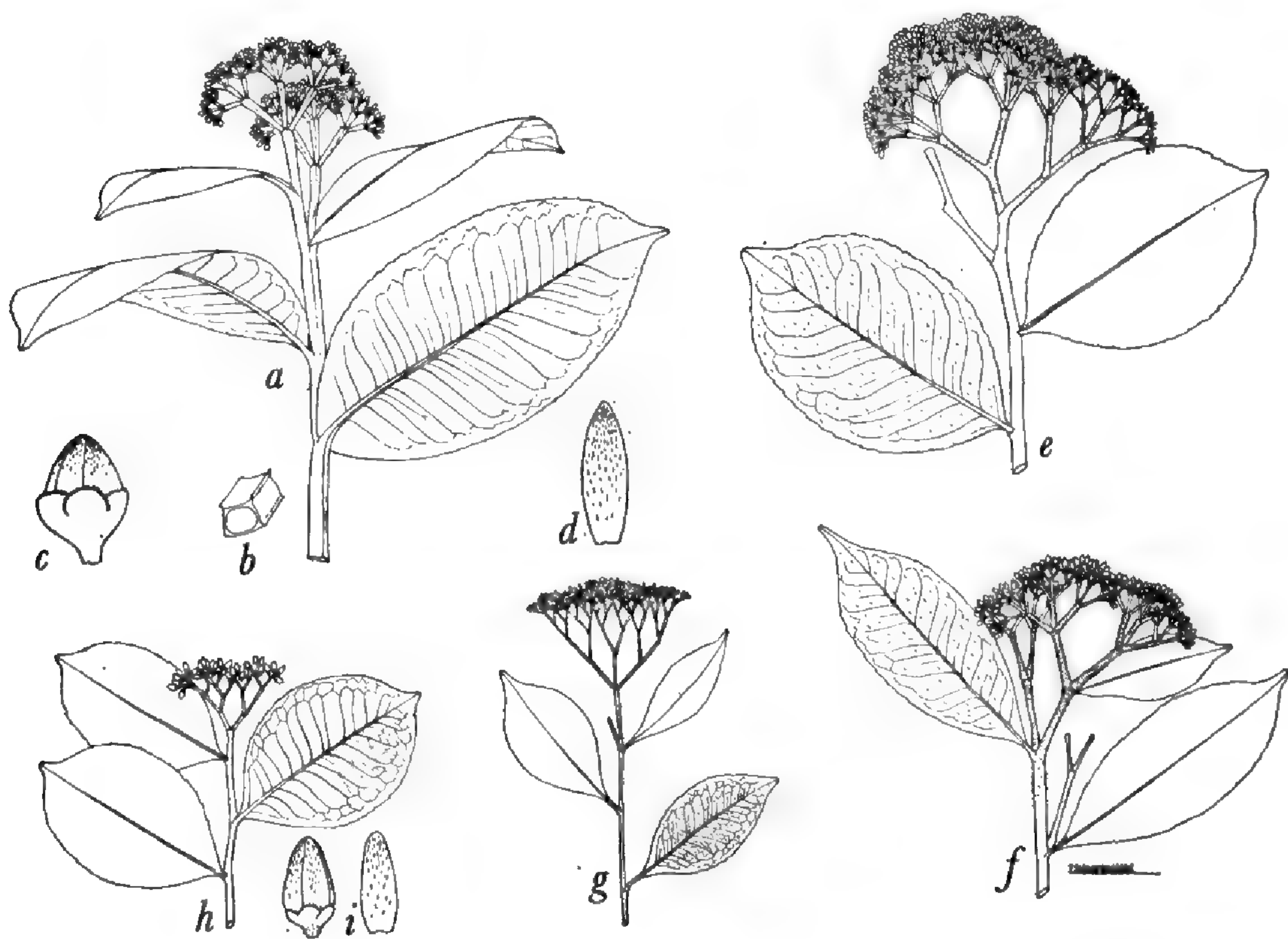


FIGURE 28.—a-d, *Humiriastrum procerum*: a, $\times \frac{1}{3}$ (Cuatr. 16615); b, section of stem; c, bud, $\times 3\frac{1}{3}$; d, petal, $\times 3\frac{1}{3}$; e, *Humiriastrum diguense* var. *diguense*, $\times \frac{1}{3}$ (Cuatr. 14956); f, *Humiriastrum diguense* var. *anchicayanum*, $\times \frac{1}{3}$ (Cuatr. 14418); g, *Humiriastrum mapiriense*, $\times \frac{1}{3}$ (Buchtien 1518); h, *Humiriastrum melanocarpum*, $\times \frac{1}{3}$ (Cuatr. 19989); i, *Humiriastrum melanocarpum*, bud and petal, $\times 3\frac{1}{3}$ (Cuatr. 19989).

longo tenui striolati minute pubescenti-hirtuli ramulis gracilibus articulatis minute hispidulis. Bracteae deciduae ovatae circa 1 mm. longae villosulae. Pedicelli crassiusculi circa 0.3 mm. longi hirtuli. Sepala ovata circa 0.6 mm. longa margine ciliata dorso hirtula. Petala (in alabastro 1 mm. longa) elliptico-oblonga glabra aestivatione contorta vel cochlearia. Stamina 20 alternatim inaequalia filamentis glabris basi coalitis. Antherae oblongae 0.5 mm. longae (in alabastro) connectivo oblongo-lanceolato. Discus 10 squamis brevibus liberis instructus. Ovarium glabrum 5-loculare loculis uniovulatis. Stylus brevis. Stigma capitatum 5-lobulatum. Drupa globosa 15–16 mm. diamitens exocarpio sublaevi tenui (0.5 mm. crasso in sicco). Endocarpium globosum circa 14 mm. diam. duro-lignosum resinoso-lacunosum ad apicem 5 minusculis foraminibus, cum 5 pseudo-operculis oblongis circa 6 mm. longis alternantibus reliqua superficie rugosa.

Type in the Herbarium of the New York Botanical Garden, collected in Sarampinni near San Carlos, region of Mapiri, Department of La Paz, Bolivia, alt. 600 m., March 7, 1927, by Otto Buchtien (No. 1518). Paratype (fruiting specimens) in the U.S. National Herbarium, No. 1905788, collected at Copacabana, about 10 km. south of Mapiri, alt. 850–950 m., Province Larecaja, Bolivia, October–November 1939 by B. Krukoff (No. 11270).

Medium-size tree with slender, minutely hirtellous-puberulous terminal branches. Leaves small, coriaceous with 3–6 mm. long, puberulous petiole. Blade glabrous, obovate or rhomboid-obovate or oblanceolate, very cuneate at base, narrowed and acutely acuminate at apex, margin serrate-crenulate; above with flat midrib, other nerves obsolete; beneath with prominent midrib, filiform secondary nerves, 8–9 pairs, little ascendent, near margin arcuate-anastomosate, minor nerves reticulate, prominulous.

Inflorescences axillary and subterminal, cymose-paniculate, longer than leaves, dichotomous or lower branches trichotomous, peduncle 1.5–2.5 cm. long, striolate and minutely hirtellous, branchlets slender, articulate, minutely hispidulous. Bracts deciduous, ovate, villous, about 1 mm. long. Pedicels thickened, about 0.3 mm. long, hirtellous. Sepals ovate, about 0.6 mm. long, ciliate at margin, hirtellous without. Petals (in bud) 1 mm. long, elliptic-oblong, glabrous, estivation contorted or cochlear. Stamens 20, alternating in length, filaments glabrous, connate at base. Anthers oblong, 0.5 mm. long (in bud), connective oblong-lanceolate. Disk formed by 10 short, free scales. Ovary glabrous, 5-locular, cells uniovulate. Style short. Stigma capitate, 5-lobulate. Drupe globose, 15–16 mm. diameter with thin, rather smooth epicarp (0.5 mm. thick); endocarp spheroid, about 14 mm. in diameter, woody, hard, with 5 minute holes at apex alter-

nating with 5 descending oblong opercles of about 6 mm. length, remaining surface rugose.

H. mapiriense is endemic of the eastern slopes of the Bolivian Andes not exceeding 1,000 m. elevation. It is a medium-size tree easily recognized by its small, firm leaves and small, globose fruit.

BOLIVIA: LA PAZ: San Carlos, Sarampinni (Región de Mapiri), 600 m. alt., *Buchtien* 1518 (NY, holotype). Larecaja, Copacabana (south of Mapiri), 850–950 m. alt., *Krukoff* 11270 (US, paratype).

11. *Humiriastrum diguense* (Cuatr.) Cuatr., comb. nov. FIGURES 28,*e–f*; 29
Sacoglottis diguensis Cuatr. Trop. Woods 96:38. 1950.

Type: *Cuatrecasas* 14956, Colombia, Valle, Río Digua.

Large tree with 60 cm. thick trunk, young branchlets puberulous. Leaves firm, coriaceous. Petiole very short (1–2 mm. long). Blade obovate-elliptic, abruptly cuneate at base, rotundate and abruptly and obtusely acuminate at apex, margin slightly and remotely crenate,

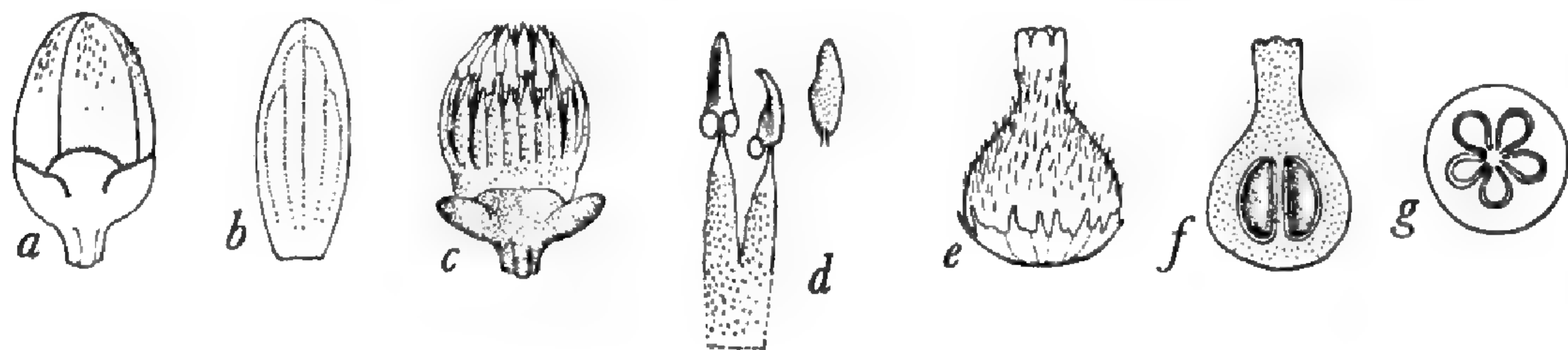


FIGURE 29.—*Humiriastrum diguense* var. *anchicayanum* (*Cuatrecasas* 14418): *a*, bud; *b*, petal; *c*, flower, petals removed, $\times 5$; *d*, detail of stamens, $\times 10$, inside view and outside view; *e*, gynoecium and disk, $\times 10$; *f*, longitudinal section of ovary, $\times 10$; *g*, transection of ovary, $\times 10$.

5.5–8.5 cm. long, 2.5–5.5 cm. broad; above dark green, glabrous, midrib marked, filiform lateral nerves little conspicuous; beneath with prominent midrib, lateral nerves ascendent, little prominent or inconspicuous, spread with minute, fine, strigose, inconspicuous hairs.

Inflorescences terminal, dichotomous-paniculate, corymbiform, longer than leaves (8–15 cm. long), branches robust, articulate, subangulate, pubescent. Bracts small, ovate, ciliate, pubescent, deciduous. Pedicels very short. Sepals 1–1.2 mm. long, suborbicular, pubescent. Petals 2.2 mm. long, elliptic-oblong, appressed, estivation quincuncial. Stamens 20, glabrous, filaments connate at base, unequal, longer 1.2 mm. alternating with shorter of 0.9 mm. length. Anthers 0.8 mm. long, connective very thick, ovoid-lanceolate, obtuse, 2 thecae elliptic, basal. Disk formed by 0.2 mm. long scales. Ovary subpyriform 1 mm. high, hirsute (at base glabrescent). Style short. Stigma 5-lobate.

Humiriastrum diguense is an important species of the rain forests of the Pacific slopes of Colombia and can be found from the hills at low altitude up to about 1,200 m. elevation. It stretches northward

to Costa Rica where a subspecies is common in the forests near Esquinas. Its wood is very hard and can be used for construction.

Key to the Subspecies and Varieties of *Humiriastrum diguense*

1. Leaves broad (5.5–8.5 × 2.5–5.5 cm.). Sepals appressed-pubescent outside. Inflorescences very robust **11a. subsp. *diguense* var. *diguense***
1. Leaves narrower (3.5–9 × 1.5–4 cm.). Sepals glabrous outside. Inflorescences more slender.
 2. Petals sparsely puberulous. Branchlets puberulous.

11b. subsp. *diguense* var. *anchicayanum*
 2. Petals subglabrous. Branchlets more densely hirtellous.

11c. subsp. *costaricense*

11a. *Humiriastrum diguense* subsp. *diguense* var. *diguense*. FIGURE 28,e

COLOMBIA: EL VALLE: Cordillera Occidental, vertiente occidental, Hoya del Río Digua, lado izquierdo; Piedra de Moler, selvas 1,140–1,180 m. alt.; gran árbol, tallo 60 cm. diám., copa grande, superiormente plana, hoja coriácea, verde oscura, brillante haz; "arrayán negro," 20–VIII–1943, *Cuatrecasas* 14956 (holotype F; isotypes US, COL, G, VALLE).

11b. *Humiriastrum diguense* subsp. *diguense* var. *anchicayanum* (Cuatr.) Cuatr., comb. nov. FIGURES 28,f; 29

Sacoglottis diguensis var. *anchicayana* Cuatr. Trop. Woods 96:39. 1950.

Type: *Cuatrecasas* 14418, Colombia, Valle, Hoya del Anchicayá.

Leaves subovate-lanceolate, acuminate, 5–9 cm. long, 2–4 cm. broad. Branchlets of inflorescence only puberulous. Sepals glabrous exteriorly, margin ciliate, about 0.8 mm. long. Petals quincuncial or cochlear, sparsely pilose, 3–3.2 mm. long, 1.2 mm. broad. Filaments united in lower third, minutely papillose, the shorter 1.2 mm., the longer ones 1.6 mm. Anthers about 0.7 mm. long with carnose, lanceolate connective and basal, ellipsoid thecae. Disk cupular with 10 long narrow teeth alternating with other irregular shorter ones.

This variety is known only from the type locality in western Colombia.

COLOMBIA: VALLE, Cordillera Occidental, Hoya del Río Anchicayá, entre Pavas y Miramar, 350–450 m. alt., bosques; árbol grande, cáliz verde, pétalos blanco-verdosos, anteras amarillentas, hoja verde oscura, craso-coriácea, 16–IV–1943, *Cuatrecasas* 14418 (holotype, F; isotypes, VALLE, COL, G, US).

11c. *Humiriastrum diguense* subsp. *costaricense* Cuatr., subsp. nov.

PLATE 14

Folia suboblango-elliptica basi cuneata apice acuminata margine crenata 3.5–6 cm. longa 1.8–3 cm. lata, petiolo circa 2 mm. longo basi incrassato, supra nervis paulo visibilibus subtus prominulis et costa eminenti, pilis tenuibus minutis adpressis sparsis inconspicuis munita. Inflorescentiae subterminales vel terminales cymoso-paniculatae trichotomae sursum dichotomae pedunculis ramisque minute hirtulis quam *S. diguensi* tenuioribus. Sepala glabra margine ciliata,

orbicularia, 0.9 mm. longa (in alabastra). Petala oblonga obtusa parce puberula (in alabastra 1.7×0.9 mm.), aestivatione cochlearia, raro contorta.

Type in the U.S. National Herbarium, No. 2085709, collected in the Esquinas forest, region between Río Esquinas and Palmar Sur de Osa, province Puntarenas, Costa Rica, January 30, 1951, by Paul H. Allen (No. 5812). Isotype in the Herbarium of Escuela Agrícola Panamericana, El Zamorano, Costa Rica.

Subspecies *costaricense* resembles greatly variety *anchicayanum*, which seems to be an intermediate form. The Costa Rican plant has narrower leaves than variety *diguense* (like *anchicayanum*), more hirtellous juvenile branches and inflorescences, glabrous sepals except for the ciliate margin, petals almost glabrous and slender, and trichotomous inflorescences that are more ascendent and abundantly ramified. The undeveloped stage of the flowers (very small buds) makes difficult a more complete study of the plant, which in the future may prove to be a different species.

About this subspecies in Costa Rica, Paul Allen states: "Very tall trees, to 140 ft. in height, with alternate, elliptic-lanceolate, glabrous leaves, the serrulate blades $1\frac{3}{4}$ – $2\frac{1}{4}$ " in length, with shortly acuminate apices and nearly sessile, cuneate bases. The very small greenish fragrant flowers are produced in terminal cymes in early January and are soon followed by the oblong or ellipsoidal, drupaceous fruits which are about 1 in. long. The reddish-brown heartwood is very hard and heavy, and is reported to be durable in contact with the ground. It is used locally for fence posts, and would appear to be suitable for general heavy construction, such as bridge timbers, railroad ties, and piling. There is some indication that the wood of this species may sometimes be confused with that of *Vantanea barbourii* and it seems possible that this may be the species represented by the sawmill sample from San Isidro del General forwarded to the Yale School of Forestry by John A. Scholten and William F. Barbour in 1944. The species is fairly frequent in the forested hills near Esquinas" (p. 317, 1956).

COSTA RICA: PUNTARENAS: Esquinas forest, between Esquinas and Palmar Sur de Osa, "níspero," tree 140 ft., flowers in bud and young fruit only, P. H. Allen 5812 (type, US, EAP).

12. *Humiriastrum procerum* (Little) Cuatr., comb. nov.

FIGURES 26,a–d; 28,a–d

Humiria procera Little, Journ. Washington Acad. Sci. 38:93, fig. 2. 1948.

Sacoglottis procera (Little) Cuatr., Trop. Woods 96:40. 1950.

Type: *Little* 6412, Ecuador, Esmeraldas, Playa de Oro.

Large tree up to 40 m. high, trunk up to 1.20 m. diameter, buttressed at base with granular bark and reddish brown, very hard wood.

Branchlets glabrous, more or less compressed, angulate, marked with longitudinal wings from decurrent leaves. Leaves rather thick, rigid, coriaceous, dark green, apparently glabrous, sessile. Blade elliptic or ovate-elliptic, rotundate or very obtuse and amplexant at base, abruptly and slightly narrowed or with short and obtuse acumen 3–8 mm. long at apex, margin almost flat or slightly revolute, sinuate-crenate, 5.5–12 cm. long, 3–7.5 cm. broad, brownish green when dry; above lustrous, glabrous with flat conspicuous midrib, secondary nerves visible and minor veins inconspicuous; beneath with prominent, more or less carinate midrib, numerous secondary nerves 2–4 mm. distant, slender, little prominent but conspicuous, spreading, near margin reticulate-anastomosate, minor veins parallel and reticulate, puberulous with thin, minute, appressed, inconspicuous hairs.

Inflorescences cymose-paniculate, corymbiform, terminal or sub-terminal, as long as leaves, peduncle robust, rigid, more or less compressed, short-pubescent, trifurcate at apex; branchlets first trifurcate upwards, dichotomous, compressed pubescent. Bracts ovate-triangular, rather acute, amplexant, ciliate, little puberulous, later deciduous. Pedicels very short (0.1 mm.), glabrous, articulate to glabrous short peduncle (0.1 mm.). Sepals 0.7 mm. long, rounded, glabrous except ciliate margin. Petals elliptic-oblong, scarcely puberulous outside, 3–3.5 mm. long, estivation quincuncial. Stamens 20, filaments almost smooth, connate at base, 10 longer 2.6 mm., shorter 2 mm. long. Anthers about 0.9 mm. long with 2 thecae at the base (one at each side), globose-ellipsoid, 0.2 mm. long, connective lanceolate, thick and angulate, cuspidate at apex. Disk 0.6–1 mm. high. Ovary globose 1 mm. high, pubescent toward apex, glabrous downward, 5-locular, cells episepal, uniovulate. Style thick, 0.6 mm. long. Stigma capitate, 5-lobate. Drupe oliviform, rounded at base, subattenuate-subacute at apex, 2.8–3.8 cm. long, 1.8–2.3 cm. in diameter. Exocarp coriaceous when dry, resinous-granulose, about 1.5 mm. thick. Endocarp up to 3.5×2 cm., woody, without or with very rare resiniferous cavities, surface rugose and alveolate, 5 deep holes at apex alternating with 5 oblong descending opercula, about 8 mm. long. Usually 1, often 2, seeds developed.

H. procerum is one of the largest trees of the rain forests of the Pacific slopes of Colombia and Ecuador. It is frequent at low elevations on hills and on uninundatable grounds along the rivers. It has a dense and dark green foliage and a buttressed trunk. The wood is extremely hard but not resistant to decay. It took two men 2 hours to cut down one of my specimens with an ax (16615). For this reason the natives resist cutting it, and chanú therefore remains more common in the forests than other more usable or practical

woods. E. L. Little writes about this species: "Large, erect tree of forest canopy, 30 to 34 m. tall and 40 cm. in diameter, according to measurements from trees felled for wood samples, but becoming larger. Heartwood dull red, turning brownish on exposure, hard and heavy. Wood fairly difficult to cut, rather harsh, readily polished, strong but brittle, not resistant to decay. Not used much because of alleged silica content, which dulls saws. Might be used for construction where not exposed to the weather. It is said that the oil seeds are edible. Common and probably widely distributed in the wet tropical forest of Esmeraldas" (p. 247, 1948).

COLOMBIA: EL VALLE: Costa del Pacífico, Río Calima, La Trojita, loma en la orilla izquierda, 30–40 m. alt.; gran árbol 40 m., 1.20 m. diám., estribos tabulares grandes; corteza dura, adherida, granulosa, pardo rojiza; madera dura, castaño-rojiza; hoja coriácea, rígida, verde oscura; capullos verdoso pálidos, "chanú," frecuente, 1–III–1944, *Cuatrecasas* 16615 (F, COL, G, US, VALLE, Y). Río Cajambre, Barco, margen izquierda de Agua Clara, Jesús, selva, 40–60 m. alt.; gran árbol, 35 m., muy coposo, tallo 60 cm. diám. con robustos estribos basilares, corteza granuloso pulverulenta, pardo rojiza clara (hacia arriba blanquecina); madera rojiza oscura; hoja coriácea, rígida, verde oscura, mate; drupas muy duras, verdes, del tamaño de oliva pequeña; corteza, madera y hojas aromáticos, "chanú," 27–IV–1944, *Cuatrecasas* 17186 (F, COL, G, VALLE, Y).

ECUADOR: ESMERALDAS: Playa de Oro, alt. 65 m., wet tropical forest, slightly cut, tree 31 m., DBH 42 cm., immature flowers green, "chanul," 1–V–1943, *Little* 6412 (holotypus US, isotypi Y); tree 32 m., DBH 42 cm., "chanul," 1–V–1943, *Little* 6413 (paratypus US, Y). 2 km. south of San Lorenzo, alt. 10 m., forest wet tropical, partly cut; tree 34 m., DBH 40 cm., common; observed at Quinindé Apr. 9 and seeds collected; good for general construction not in contact with ground; seeds like pecan; flower buds greenish, twigs winged, "chanul," 21–IV–1943, *Little* 6320 (US, Y). Quinindé, alt. 65 m., wet tropical forest (only fruit, from ground), "chanul," 9–IV–1943, *Little* 6233 (US).

13. *Humiriastrum melanocarpum* (Cuatr.) Cuatr., comb. nov.

FIGURES 26,*r–t*; 28,*h–i*

Sacoglottis melanocarpa Cuatr., Trop. Woods 96:37. 1950.

Type: *Cuatrecasas* 19989, Colombia, Valle, Buenaventura.

Large tree with grayish or brownish rugulose terminal branchlets. Leaves coriaceous, subsessile, glabrous. Blade obovate, cuneate and tapering to a very short petiole at base, subrotund but abruptly, shortly and obtusely acuminate, the margin slightly crenate with small glands; 4–7 cm. long, 2.5–4.5 cm. broad, above green, nitid with conspicuous midrib and obsolete lateral nerves, beneath with prominent midrib, secondary nerves spreading, slightly prominent, near the margin anastomosate.

Inflorescence axillary, subterminal, cymose-paniculate, 2–4 cm. wide, peduncle terete, glabrous; branches dichotomous, articulate, puberulous, 2–6 mm. long; bracts deciduous; pedicels up to 1 mm. long. Sepals 0.5 mm. long, almost free, ovate, obtuse, sparsely puber-

ulous with ciliate margin. Petals oblong, slightly broadened at base, sparsely pilose, 2.6 mm. long, 1 mm. broad. Stamens 20, glabrous, longer filaments about 2 mm. long, shorter 1.5 mm. long, alternating, linear, acute, united at base. Anthers 0.7 mm. long, glabrous, cordate-lanceolate, connective thick, subobtuse, 2 thecae suborbicular, divergent at base. Disk formed by several 0.4 mm. long dentate scales. Ovary ovate-orbicular, 1.1 mm. high, glabrous, 5-locular or 2-3-locular through abortion, cells uniovulate. Drupe ovoid or ovoid-oblong, apiculate, acute, black and lustrous when ripe, 16-18 mm. long, 10-13 mm. diameter. Endocarp woody, oblong-ovoid sharply acute at apex with 5 minute foramina alternating with 5 small, oblong, descending opercules not surpassing half of the fruit, 14-15 mm. long, 7-8 mm. in diameter.

A very distinct species endemic to the Pacific coast of Colombia; it is known only from the cited collections.

COLOMBIA: EL VALLE; Costa del Pacífico, Buenaventura, Quebrada de Aguadulce, 0-5 m. alt.; gran árbol; hoja coriácea, delgada, rígida, verde medio y brillante haz, verde claro envés; perianto verde amarillento claro; fruto ovoideo, apiculado, negro brillante, 18×13 mm., "chanú," 24-II-1946, *Cuatrecasas* 19989 (F, holotype; COL, G, W, VALLE, isotypes). Buenaventura, Quebrada de San Joaquín, 0-10 m. alt.; árbol grande; hoja coriácea, subrígida, verde; frutos verdes, oblongos, apiculados, 16-18×9 mm., "chanú," 22-II-1946, *Cuatrecasas* 19909 (F, COL, G, W, VALLE, paratypes).

7. *Schistostemon*

Schistostemon (Urban) Cuatr., gen. nov.

Saccoglottis subgen. *Schistostemon* Urb. in Mart. Fl. Bras. 12(2):443, 445. 1877.

Saccoglottis Sect. *Schistostemon* (Urb.), Reiche in Engl. & Prantl, Pflanzenfam. 3(4):37, fig. 32. 1890.

Sacoglottis Sect. *Schistostemon* (Urb.), Winkl. in Engl. & Harms, *ibid.*, 19a:128, fig. 59-J. 1931.

Humirium Benth. in Hook. London Journ. Bot. 2:374. 1843 (in part); in Hook. Journ. Bot. Kew Misc. 5:102. 1853.

Sepals 5, suborbicular, more or less united at base. Petals 5, free, linear or oblong, thick, estivation quincuncial, cochlear or contorted. Stamens 20, glabrous, very unequal; 5 opposite sepals longer, trifurcate at apex and triantheriferous, 5 opposite petals less long, entire and monantheriferous, 10 intermediate shorter, monantheriferous; filaments more or less complanate and thickish, united in lower part up to middle. Anthers ovate or ovate-lanceolate, thecae 2, unilocular, ellipsoid or oblong, affixed on lower side, connective thick, more or less lanceolate rarely obtuse. Occasionally lateral anthers of trifurcate stamens are sterile. Disk cupular, dentate, or rarely of 10 free scales. Ovary 5-locular, cells uniovulate. Carpels opposite sepals. Ovules anatropous with ventral raphe, pending from inner angles of ovary. Styles thick, short, up to 1 mm. long. Stigma capitate and

5-lobate. Drupe rather large, smooth, with thick carnous or subcoriaceous (when dry) exocarp. Endocarp woody, more or less bullate with 10 very narrow, slightly apparent furrows, filled with many globose resinous cavities; 5 septa in transection irregular and more or less conspicuous; usually only 1 or 2 seeds developed, apparently indehiscent, but the germinating embryos pushing away longitudinal broad valves; these valves going from apex to base of endocarp, apparently covering its surface; ribs between valves very thin; germinal subapical foramina not observed. Evergreen trees with coriaceous or subcoriaceous, simple, alternate, petiolate, or sessile leaves with usually more or less crenate margin. Inflorescences axillary or subterminal, paniculate, with dichotomous or trichotomous branching. Bracts persistent. (See also figs. 3, 30, and 31.)

Type species: *Schistostemon oblongifolium* (Benth.) Cuatr.

The name "Schistostemon" is derived from the Greek "schistos" (split) and "stemon" (filament), an allusion to the five trifurcate stamens of this genus.

Schistostemon has seven known species and one subspecies mainly distributed throughout the Guianas and the middle and northwestern Amazon Basin.

Key to the Species of *Schistostemon*

1. Young branchlets minutely pilose.
 2. Leaves oblong (4 times as long as broad), acuminate, crenate, minutely papillose and sparsely pilose beneath. Inflorescence very small, dichotomous. Sepals and petals pubescent outside. Drupe elongate, subfusiform or fusiform. Petiole 5–7 mm. long. . . . **1. S. oblongifolium**
 2. Leaves ovate, lanceolate or attenuate-elliptic (less than 3 times as long as broad), subentire, glabrous, not papillose.
 3. Connective of the anthers obtuse. Calyx glabrous except for the minutely ciliate margin. Leaves very rigid, strongly and minutely reticulate. Petiole 2–5 mm. long. Petals pubescent outside.
 2. **S. auyantepuiense**
 3. Connective of the anthers ovate-attenuate, acute. Calyx more or less pilose and margin long-ciliate. Leaves less rigid with prominulous, lax reticulum. Petiole 2–8 mm. long. **3. S. reticulatum**
 4. Petals 4–4.5 mm. long, appressed-pubescent. Sepals sparsely pubescent. Leaves 6–12.5×4.5–7.5 cm., ovate or elliptic. Petiole 3–8 mm. long **3a. S. reticulatum** subsp. **reticulatum**
 4. Petals 3.5–4 mm. long, subglabrous, with scarce hairs at apex. Sepals densely hispidulous. Leaves smaller, 4–9.5×2–5 cm., sublanceolate. Petiole 2–5 mm. long **3b. S. reticulatum** subsp. **froesii**
1. Young branchlets glabrous.
 5. Petioles 0–1 mm. long. Leaf blade thick-coriaceous, broadly elliptic or suborbicular, rounded or retuse at apex, margin subentire, sheath (or very short petiole) very thick, venation lax reticulate and prominulous. Drupe globose, 3–4.5 cm. diameter, endocarp 2.6–3.4 cm. . **4. S. retusum**

5. Petioles 6–14 mm. long. Leaf blade more or less attenuate at apex, more or less crenate at margin.
6. Leaves minutely and conspicuously reticulate above, secondary nerves prominulous and veins slightly conspicuous beneath. Petals thick, glabrous, subobtuse or subacute, deciduous. Sepals broad, subcoriaceous. Inflorescences with alternate branches or lower ones dichotomous; peduncle 1–3 cm. long. Drupe oblong-ovoid, 3.5–4×2–2.8 cm. Disk with united scales 5. **S. macrophyllum**
6. Leaves prominently venose-reticulate on both sides. Inflorescence dichotomous. Petals and sepals submembranous, persistent.
7. Petals glabrous. Sepals ciliolate at margin. Peduncle of inflorescence 3.5–6 cm. long. Disk with free scales. Drupe unknown. 6. **S. dichotomum**
7. Petals hirtellous-pubescent with retrorse hairs. Sepals hirtellous pubescent, margin ciliate. Peduncle of inflorescence 1.5–3 cm. long. Disk annular, short, dentate. Drupe ovoid-ellipsoid, 2.6×2.3 cm. 7. **S. densiflorum**

1. **Schistostemon oblongifolium** (Benth.) Cuatr., comb. nov.

FIGURES 30,*h-i*; 31,*g-i*; 32,*a*

Humirium oblongifolium Benth. in Hook. Journ. Bot. Kew Misc. 5:103. 1853.

Sacoglottis oblongifolia (Benth.) Urb. in Mart. Fl. Bras. 12(2):447 pl. 93.

1877.—Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 4:26,29. 1937.

Type: *Spruce* s.n., Brazil, Amazonas, Barcellos.

Small tree. Branchlets terete, ochraceous-brownish, lenticellate, minutely hirtellous-pubescent or puberulous. Leaves firm, coriaceous with 5–7 mm. long, thickened and more or less puberulous petiole. Blade elliptic-oblong, sublanceolate, rounded or obtuse at base, slightly decurrent along petiole, narrowed toward and acuminate at apex, margin slightly serrate-crenate, 7–17 cm. long, 3–4.8 cm. broad, acumen obtusely triangular, up to 1.5 cm. long; above rather lustrous, glabrous or flat midrib puberulous toward base, secondary nerves obscurely prominulous, vein-reticulum lax, more or less conspicuous; dull beneath, minutely papillose and with abundant, although diffuse, subappressed hairs, midrib prominent, minutely pubescent or puberulous, 9–12 pairs of spreading and prominent secondary nerves near margin arcuate-anastomosate, veins forming a rather prominent reticulum.

Inflorescences axillary, short-cymose-paniculate, dichotomous (rarely trichotomous), peduncle robust, 4–10 mm. long, hirtellous, short branches rather thick, hirtellous. Bracts persistent, ovate, obtusish, amplexant, pubescent, densely ciliate, 1.5–0.5 mm. long. Sepals 1 mm. long, rotund, imbricate, minutely pubescent, densely ciliate. Petals greenish, rather thick, oblong, attenuate toward apex, subacute, subappressed-pubescent, 4–5 mm. long, 1.5 mm. broad. Stamens 20,

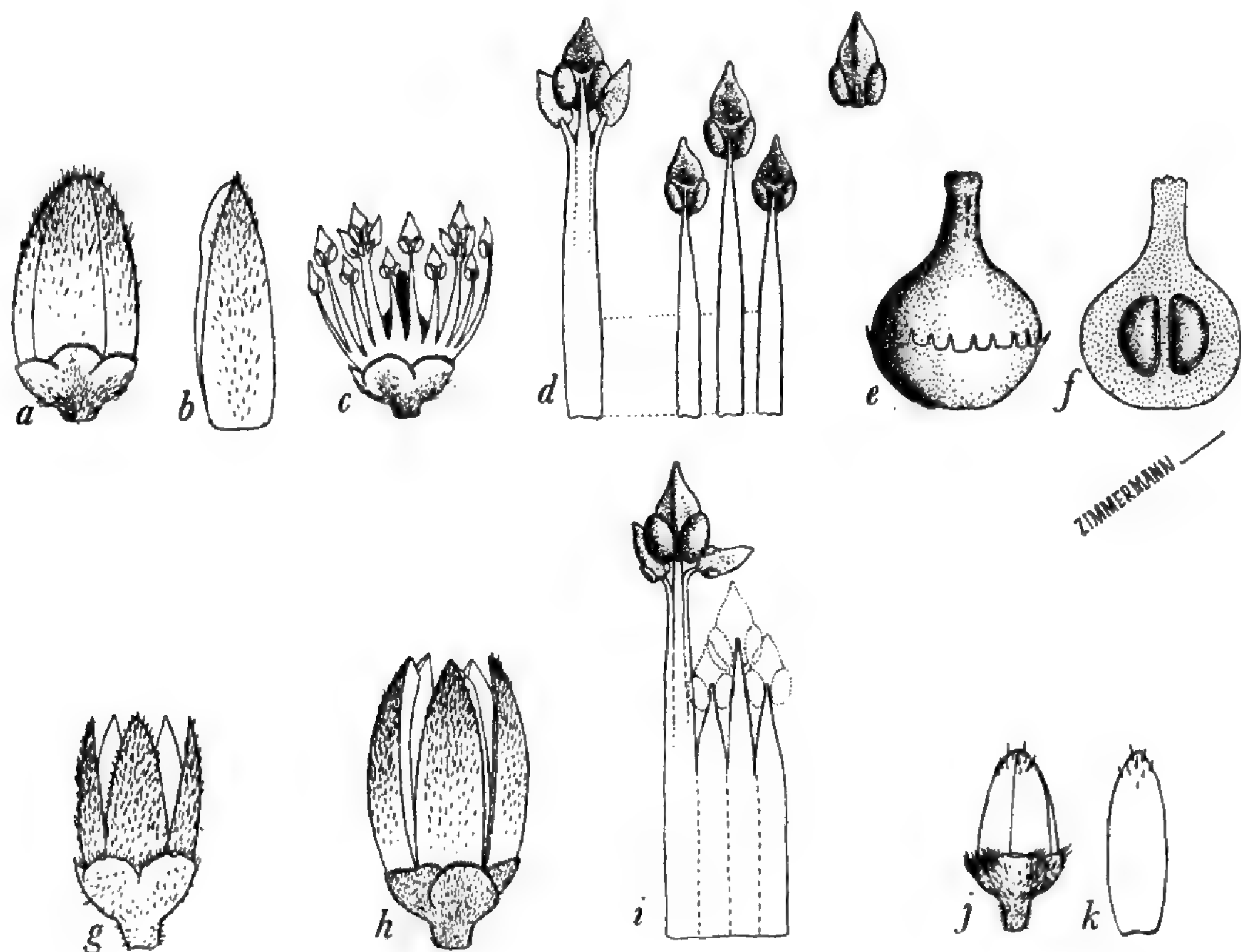


FIGURE 30.—*a-f*, *Schistostemon retusum* (Fröes 22747): *a*, bud; *b*, petal; *c*, open flower with petals removed, $\times 5$; *d*, stamens from outside and one another from inside, $\times 10$; *e*, gynoecium and disk, $\times 10$; *f*, longitudinal section of ovary, $\times 10$. *g*, *Schistostemon reticulatum* subsp. *reticulatum* (Ducke 23819), opening bud, $\times 5$. *h-i*, *Schistostemon oblongifolium* (Fröes 21090): *h*, opening bud, $\times 5$; *i*, detail of staminal tube, the longer stamen from inside, $\times 10$. *j-k*, *Schistostemon reticulatum* subsp. *froesii* (Fröes 21370): *j*, bud $\times 5$; *k*, petal, $\times 5$.

glabrous, filaments 2.7–3.5 mm. long united in tube up to middle, 5 longer ones short-trifurcate and bearing 3 anthers, 5 medium and 10 smaller alternating, undivided and each with one anther; sterile filaments often present. Anthers ovate-lanceolate, about 0.9 mm. long, thecae oblong, about 0.4 mm. long, connective thick, angulate, lanceolate. Disk rather thick, cupuliform, about 0.6 mm. high, with dentate margin. Ovary ovoid, glabrous, about 1.4 mm. high, 5-locular, cells uniovulate. Style thick, 0.5–0.6 mm. long. Stigma capitate, 5-lobate. Ovules about 0.6 mm. long. Drupe oblong, subfusiform, 4–4.5 cm. long, 1.3–1.5 cm. broad, attenuate at both ends, apex acute, exocarp glabrous, almost smooth, thick, fibrous, easily loosening; endocarp woody, subfusiform, rather smooth or slightly bullate, about 3×1.2 cm., obtuse at base, apiculate at apex.

S. oblongifolium is a small tree found along the rivers of the Rio Negro in Brazil and southern Venezuela.

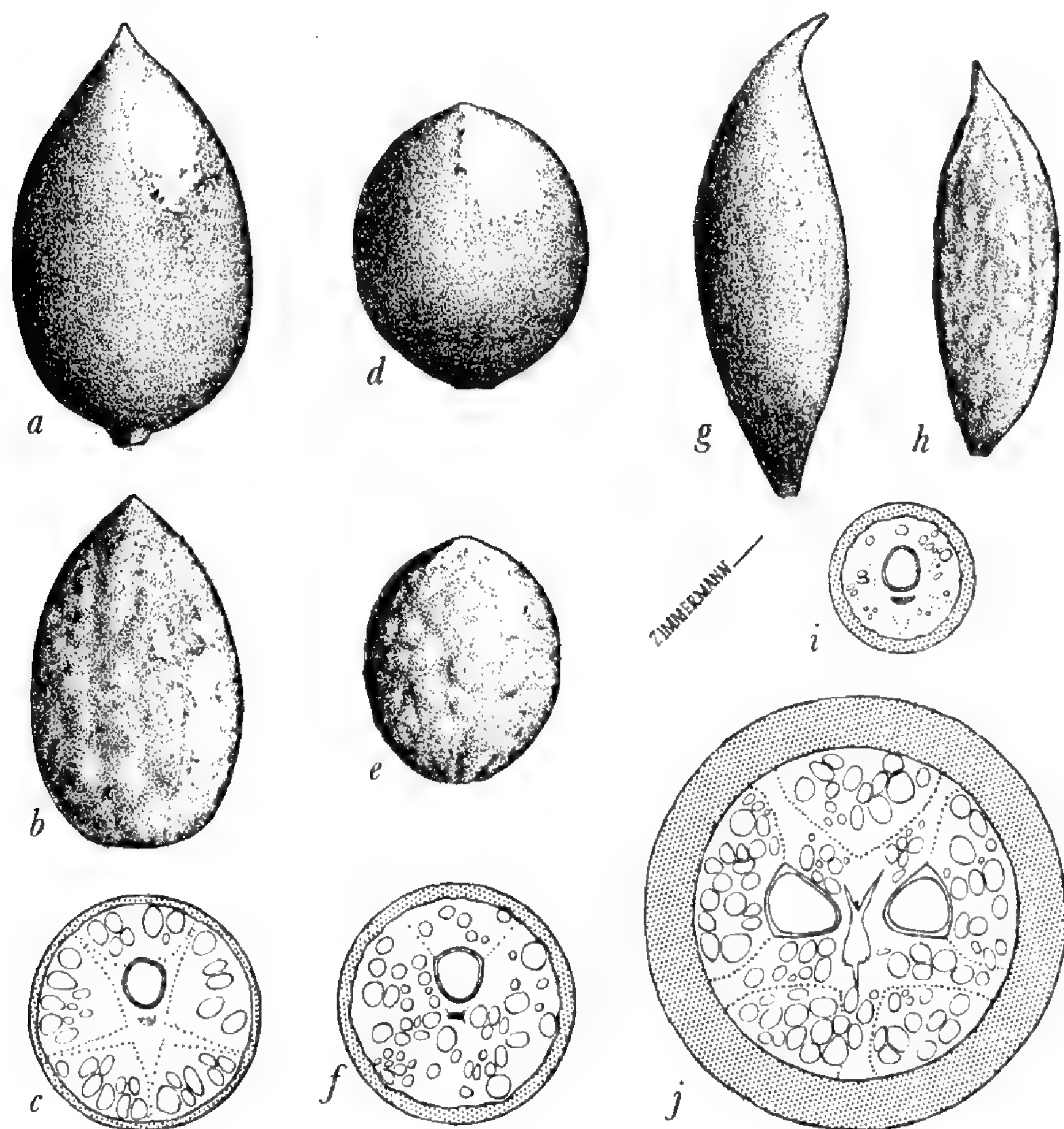


FIGURE 31.—*a-c*, *Schistostemon macrophyllum*, $\times 1$ (Ducke 1175): *a*, fruit; *b*, endocarp; *c*, transection. *d-f*, *Schistostemon densiflorum*, $\times 1$ (Persaud 102): *d*, fruit; *e*, endocarp; *f*, transection. *g-i*, *Schistostemon oblongifolium*, $\times 1$ (Baldwin 3187): *g*, fruit; *h*, endocarp; *i*, transection. *j*, *Schistostemon retusum*, transection, $\times 1$ (Ducke 30131).

VENEZUELA: AMAZONAS: Río Negro, prope San Carlos, 1853–54, *Spruce* 3073 (GH, P, NY). Ad flumen Casiquiari, Vasiva et Pacimoni, 1853–54, *Spruce* 3094 (NY). “In ripis Vasiva, XII–1853, one specimen taken from another tree with narrower leaves, looks different from rest”; “there was no more in flower” (Herb. Benthamianum), *Spruce* 3194 (BM, K).

BRAZIL: AMAZONAS: Rio Negro, Serra de São Gabriel beira d’agua; arvore pequena, 1–V–1947, *Pires* 588 (NY, IAN). Rio Negro, San Gabriel, 18–IX–1928, *Tate* 142 (NY, US). São Gabriel, Igarapé Curucuh, 27–XI–1945, *Fróes* 21437 (IAN, K, NY, US). São Gabriel, ad ripas periodice inundatas; arbor parva, floribus viridibus, 28–X–1932 (flores), 16–II–1936 (fructus), *Ducke* 23817 (US, P, S, U). Rio Negro, Jerusalem, terreno arenoso, beira rio não inundavel, arbusto 3 m. em feixe; flores abundantes branco verde perfumativo, 1–VIII–1955, *Fróes* 21090 (NY, IAN, K, US). Rio Negro, inter Barcellos et San Isabel, XII–1851, *Spruce* 1969 (isotypes, NY, M, GH). Rio Negro, mouth of Rio Içana; tree to 20 ft. high, 5–III–1944, *Baldwin* 3187 (IAN, US). In flumini Negro superioris ripis, XII–1854 (Herbarium Benthamianum), *Spruce* s.n. (holotype, K). Rio Negro prope San Gabriel do Cachoeiros, VIII–1852, *Spruce* 2419 (P).

2. *Schistostemon auyantepuiense* Cuatr., sp. nov. FIGURES 32, b; 36, o-p; PLATE 15

Arbor ramis terminalibus minutissime pilosulis.

Folia rigide coriacea fragilia glabra. Petiolus brevis robustus inferne incrassatus 2-5 mm. longus. Lamina ovata vel ovato-elliptica basi obtusa cuneata apice attenuata acuminataque acuta raro obtusata, margine levissime crenata subintegra glandulis minutis sparsis basi plus minusve conspicue biglandulosa; supra nitida costa ampla prominula nervis nervulisque conspicue prominuleque reticulatis; subtus costa eminenti, nervis secundariis tenuibus sed prominentibus 8-9 utroque latere arcuato anastomosatis nervulis minutum reticulum prominentem formantibus. 4-8 cm. longa, 2.5 cm. lata.

Inflorescentiae axillares subterminales breves cymoso-paniculatae pedunculo 2-10 mm. longo breviter minuteque hirtulo-pubescenti ramulis semel dichotomis vel omnibus alternis crassiusculis striatis minute pilosis. Bractee triangulares amplexantes persistentes acutae 1-1.5 mm. longae margine minute ciliolatae, dorso minute papillosae et sparse pilosulae. Pedicelli crassiusculi minute piloso-



FIGURE 32.—a, *Schistostemon oblongifolium* (Ducke 23817); b, *Schistostemon auyantepuiense* (Vareschi & Foldats 4673); c, *Schistostemon reticulatum* subsp. *froesii* (Fróes 21370); d, *Schistostemon retusum* (Fróes 22747), $\times \frac{1}{2}$.

hispiduli 0.5 mm. longi. Calyx 5 sepalis crassis rotundatis margine tenuibus minuteque ciliatis circa 1.5 mm. longis basi breviter coalitis dorso minute papilloso et glabris. Petala cochlearia vel contorta oblonga acutiuscula crassa 4–4.5 mm. longa 1.5 mm. lata dorso papillosa minuteque pubescentia. Stamina 20 filamentis crassiusculis complanatis tertio inferiore in tubum connatis 5 longioribus (3 mm.) oppositisepalis apice trifidis triantheriferis antheris tribus fertilibus, 5 mediis brevioribus (2.5 mm.) 10 intermediis minoribus (2.2 mm.). Antherae glabrae ovatae 0.5–0.7 mm. bithecae, thecis unilocis oblongo ellipsoideis, connectivo crasso obtuso vel obtusissimo. Discus membranaceus cylindraceus margine dentatus circa 0.8 mm. altus. Ovarium pyriforme glabrum in stylum 0.5 mm. longum attenuatum 5-loculare loculis uniovulatis. Stigma breviter capitatum 5-lobulatum.

Type in the Herbarium of Instituto Botanico, Caracas, Venezuela, collected in montane forests above the Guayaraca camp, about 1,100 m. elevation, on Mount Auyantepui, State of Bolívar, Venezuela, April 1956, by Volkmar Vareschi and Foldats (No. 4673).

Tree with minutely pilose terminal branchlets. Leaves stiffly coriaceous, glabrous. Petiole short, robust, 2–5 mm. long, the base thickened. Blade ovate or ovate-elliptic, obtusely cuneate at base, attenuate and acuminate at apex, rarely obtuse, margin slightly crenate, subentire with minute punctiform glands, more or less conspicuously biglandular at base; 4–8 cm. long, 2.5–5.2 cm. broad; lustrous above with broad prominulous midrib, other nerves prominulous, conspicuous, reticulate; midrib prominent beneath, secondary nerves slender but prominent, 8–9 pairs, arcuate, anastomosate, veins forming minute prominent reticulum.

Inflorescences axillary, subterminal, short, cymose-paniculate, peduncle 2–11 mm. long, minutely hirtellous-pubescent, branchlets first dichotomous or all alternate, rather thick, striate, minutely pilose. Bracts amplexant, persistent, triangular, acute, 1–1.5 mm. long, ciliolate at margin, minutely papillose and sparsely pilose outside. Pedicels rather thick, minutely pilose-hispidulous, 0.5 mm. long. Sepals thick, rounded, about 1.5 mm. long, thin and ciliolate at margin, papillose and glabrous outside, connate at base. Petals 4–4.5 mm. long, 1.5 mm. broad, oblong, subacute, densely papillose and minutely pubescent; estivation cochlear or contorted. Stamens 20, filaments thick, complanate, lower third connate in tube, 5 longer (3 mm.) opposite sepals, shortly trifurcate at apex and triantheriferous (3 anthers fertile), 5 intermediate shorter (2.5 mm.) and 10 shortest (2.2 mm.) entire and monantheriferous. Anthers glabrous, ovate, 0.5–0.7 mm. long, thecae unilocular, oblong-ellipsoid, connec-

tive thick, obtuse or very obtuse. Disk membranaceous, cylindrical, about 8 mm. high, margin dentate. Ovary pyriform, glabrous. Style 0.5 mm. long, attenuate, 5-locular, cells uniovulate. Stigma capitate, 5-lobate.

By its smaller and more rigid leaves and almost obovate connective of its anthers, *S. auyantepuiense* differs essentially from the closely related *S. reticulatum*. It is known only from Auyantepuí, one of the Venezuelan Guayana hills, where it grows in the low forest of the upper mountain. *S. auyantepuiense* is a xeromorphic endemic characterized by its rigid, brittle, glossy, prominently reticulate leaves; it is the species of the genus found at the highest elevation.

VENEZUELA: BOLÍVAR: Cerro Auyantepuí, arriba del campamento Guay-araca, 1,100 m. alt., Vareschi & Foldats 4673 (holotype, VEN).

3. *Schistostemon reticulatum* (Ducke) Cuatr., nov. comb.

FIGURES 30,*g*; 33,*h*

Sacoglottis reticulata Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 1:206. 1935; 4:26, 29. 1937.

Type: *Ducke* 23819, Brazil, Amazonas, São Paulo de Olivença.

Medium-size tree with minutely puberulous terminal branchlets. Leaves firm, coriaceous, glabrous. Petiole thick, short, 3–8 mm. long. Blade ovate or elliptic, obtuse or subrotundate at base, abruptly attenuate, obtusely acuminate at apex, margin slightly crenulate, 6–12.5 cm. long, 4.5–7.5 cm. broad; above nitid, pale green, midrib slightly prominent, 8–9 pairs of secondary nerves prominulous, subpatulous, near margin arcuate-anastomosate, smaller veins prominently reticulate; midrib thick and prominent beneath, secondary nerves prominent, reticulation lax, more or less prominulous.

Inflorescences axillary, cymose-paniculate, dichotomous at base, peduncle compressed, striate, short-pubescent, branchlets minutely pubescent-hirtellous. Bracts amplexant, persistent, ovate-triangular, inferior obtuse, superior acute, 1–0.5 mm. long. Sepals 1.4 mm. long, submembranous, imbricate, ovate, obtuse or subrotundate, puberulous, margin ciliate, apex with small callous gland. Petals greenish, oblong, rather acute, appressed-pubescent, 4–4.5 mm. long, 1–1.5 mm. broad, estivation cochlear. Stamens 20, glabrous, filaments 2.2–3 mm. long, complanate, united in tube at base, 5 longer shortly trifurcate and triantheriferous. Anthers ovate, about 0.8 mm. long, thecae elliptic-oblong 0.3–0.4 mm. long, connective ovate, acuminate. Ovary subglobose, glabrous. Style short (0.4 mm. long), thick. Stigma thick, capitate, 5-lobate.

Only fruit of subspecies *froesii* is known. The type specimen looks glabrous at first sight, but careful examination of the only available branchlet shows the existence of some minute hairs near the end.

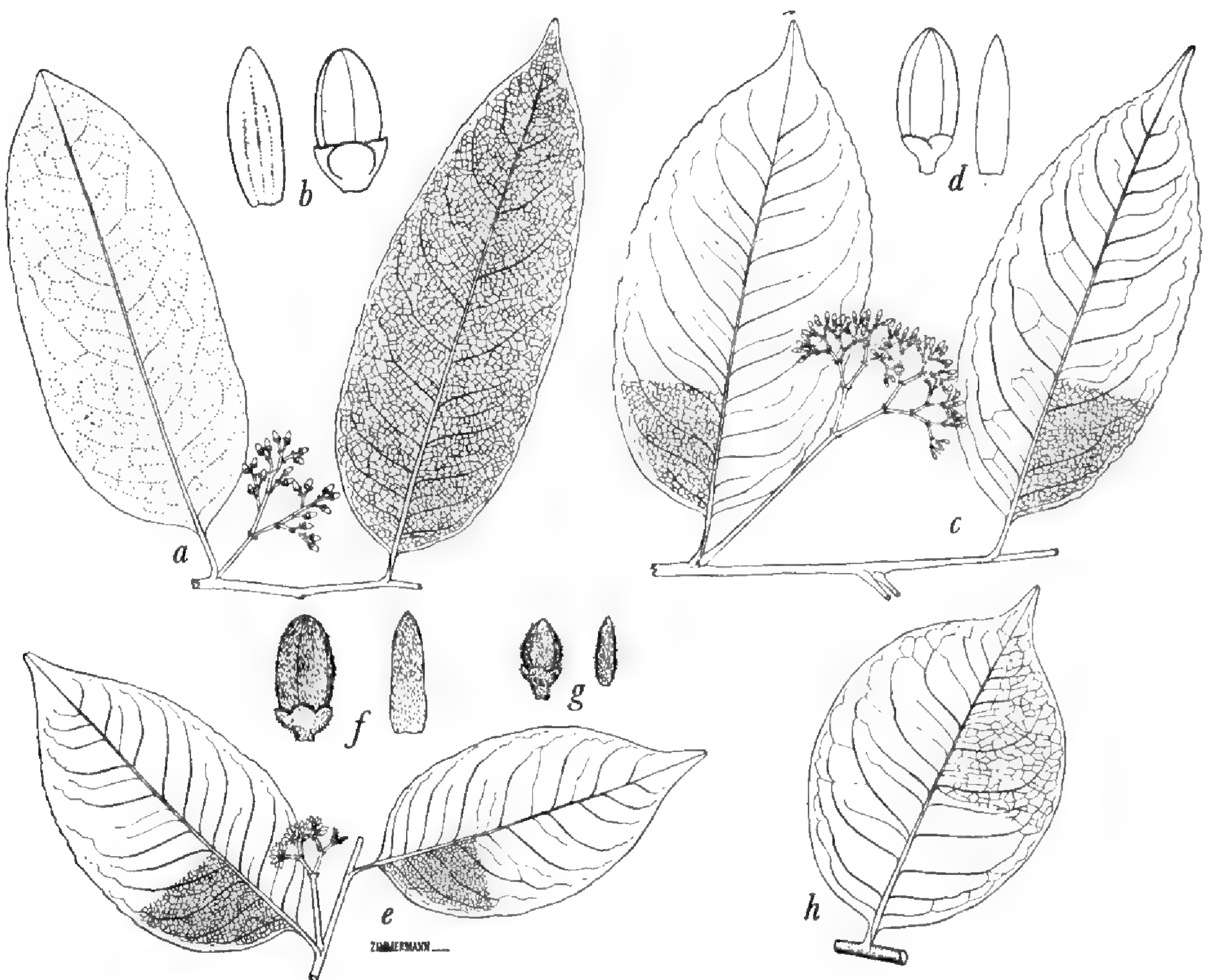


FIGURE 33.—*a*, *Schistostemon macrophyllum*, $\times \frac{1}{3}$ (Ducke 23816); *b*, *Schistostemon macrophyllum*, petal and bud, $\times 3\frac{1}{2}$; *c*, *Schistostemon dichotomum*, $\times \frac{1}{3}$; *d*, *Schistostemon dichotomum*, bud and petal, $\times 3\frac{1}{2}$; *e*, *Schistostemon densiflorum*, $\times \frac{1}{3}$ (Schomburgk 543); *f*, *Schistostemon densiflorum*, bud and petal, $\times 3\frac{1}{2}$ (Schomburgk 543); *g*, *Schistostemon densiflorum*, bud and petal, $\times 3\frac{1}{2}$ (Boschweyen 2068, "*S. kaboeriensis*"); *h*, *Schistostemon reticulatum* subsp. *reticulatum*, leaf, $\times \frac{1}{3}$ (Ducke 23819).

3a. *Schistostemon reticulatum* subsp. *reticulatum* FIGURES 30,*g*; 33,*h*

BRAZIL: AMAZONAS: São Paulo de Olivença (Rio Solimões), silva non inundabilis; arbor medioeris floribus viridibus, 3-X-1931, Ducke 23819 (US, isotype).

PERU: LORETO: Mishuyacu, near Iquitos, alt. 100 m., tree 15 m., flowers yellow-green, fruit edible, very "aromatic," "parinari," VII-1930, Klug 1564 (US).

3b. *Schistostemon reticulatum* subsp. *froesii* Cuatr., subsp. nov.

FIGURES 30,*j-k*; 32,*c*; PLATE 16

Arbor parva ramulis terminalibus brunneis vel rufescentibus minute hispidopubescentibus.

Folia firme crasseque coriacea simplicia. Petiolus 2–5 mm. longus supra planus vel canaliculatus basi vaginatus juvenili pilosulus demum glabratus. Lamina glabra ovato-lanceolata basi subrotundata et breviter angusteque cuneata apicem versus gradatim attenuata et subacuta raro obtusa, margine integra vel levissime sinuata, 4–9.5 cm.

longa 2–5 cm. lata; supra nitida viridula costa plana nervis secundariis tertiariisque laxe reticulatis prominulis; subtus costa crassa elevata nervis secundariis 6–7 utroque latere prominentibus nervulis prominulis laxe reticulatis.

Inflorescentiae breves axillares inferne dichotomae pedunculo 1–6 mm. longo robusto striato minute hispido-pubescenti, ramulis brevibus dense hispidulis, bracteis bracteolisque ovatis subacutis vel obtusis pubescenti-hirtulis 1–1.5 mm. longis amplexantibus persistentibus. Pedicelli crassiusculi hispiduli circa 0.5 mm. longi. Sepala subrotundata 1 mm. longa 1.5 mm. lata basi coalita extus hirtulo-pubescentia, margine longe ciliata apice calloso-glanduloso excepto. Petala crassiuscula oblonga subacuta 3.5–4 mm. longa 1.5 mm. lata subglabra tantum dorso sursum parce pilosula, praefloratione cochleari. Stamina 20 glabra filamentis margine saepe leviter papillosis complanatis basi in tubum 1 mm. altum vel ultra coalitis, 5 episepalis longioribus (2.5 mm.) tridentatis triantheriferis (antheris lateralibus sterilibus), 5 epipetalis (2 mm. long.) monantheriferis et 10 alternantibus brevioribus monantheriferis (1.5 mm. long.). Antherae ovato-acuminatae circa 0.7 mm. longae thecis unilocularibus oblongo-ellipsoideis connectivo crasso ovato-acuminato. Discus cupuliformis 0.8 mm. altus margine denticulatus. Ovarium glabrum subglobosum 5-loculare loculis uniovulatis. Stylus 0.3–0.4 mm. longum. Stigma capitatum.

Type in the Herbarium of the New York Botanical Garden, collected at Foz de Cairay, Serra de Tunuhy, alt. 500 m., Içana drainage, State of Amazonas, Brazil, November 13, 1945, by Ricardo de Lemos Fróes (No. 21370). Isotype in the U.S. National Herbarium, No. 1496431, in Kew Herbarium and in Instituto Argonómico do Norte.

Small tree with brownish or reddish and minutely hirtellous terminal branchlets. Leaves firm, rather thick-coriaceous with 2–5 mm. long pilose or glabrate petiole. Leaf blade ovate-lanceolate, rounded and shortly angustate-cuneate at base, gradually attenuate and subacute (rarely obtuse) at apex, entire or slightly sinuate at margin, 4–9.5 × 2–5 cm.; above lustrous, greenish with flat midrib and prominulous secondary and tertiary nervation; beneath midrib thick, prominent, 6–7 pairs of secondary nerves prominent, reticulation lax and prominulous.

Inflorescences short, axillary, dichotomous below, peduncle stout, striate, minutely hispidulous, branchlets small, densely hispidulous, bracts persistent, amplexant, ovate, subacute or obtuse, hirtellous. Pedicels rather thick, hispidulous, about 0.5 mm. long.

Sepals subrounded, 1 mm. long, united at base, hirtellous outside, ciliate at margin, with callous gland at apex. Petals thickish, oblong, subacute, 3.5–4 × 1.5 mm., subglabrous, scarcely pilose, up-

wards outside, estivation cochlear. Stamens 20, glabrous, filaments complanate, more or less papillose, united in tube 1 mm. high at base, 5 episealous longer, tridentate, triantheriferous, 5 epipetalous shorter, uniantheriferous and other 10 still shorter alternating. Anthers ovate-acuminate, about 0.7 mm., with unilocular oblong-ellipsoid thecae and carnose, ovate-acuminate connective. Disk cupuliform 0.8 mm. high, denticulate. Ovary glabrous, subglobose, 5-locular, cells uniovulate. Style 0.3-0.4 mm. long. Stigma capitate, 5-lobate. Ovules anatropous with ventral raphe, suspended.

This subspecies differs from *reticulatum* in its smaller, more rigid leaves, which are more cuneate at the base, and in the almost glabrous petals and the densely hispidulous sepals. The terminal branchlets are conspicuously hispid-pubescent seen under the microscope. *S.r. froesii* represents a xeromorphic subspecies of *S. reticulatum* and is adapted to the hills near Rio Içana.

BRAZIL: AMAZONAS: Serra de Tunuhy, 500 m. alt., arvore 3 m., Foz do Cairay, Rio Içana, *Fróes* 21370 (type).

4. *Schistostemon retusum* (Ducke) Cuatr., comb. nov.

FIGURES 30,*a-f*; 31,*j*; 32,*d*; PLATE 17

Sacoglottis retusa Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 4:26, 29, pl. 2, fig. d. 1938.

Type: *Ducke* 30131, Brazil, Amazonas, Rio Curicuriary.

Small or medium-size tree with glabrous branchlets. Leaves stiff, thick-coriaceous, sessile or subsessile with extremely short, vaginate-thickened petiole. Blades broadly elliptic or suborbicular-elliptic or slightly obovate, rounded or very obtuse at base, at apex rounded, often retuse, rarely obtusely attenuate, margin subentire, 6-15 cm. long, 4.5-10 cm. broad; above almost smooth to conspicuously nerved with small prominent midrib and lateral nerves and veins more or less prominulous; prominent thick midrib beneath, 8-9 secondary nerves on each side, prominent, subspreading, near margin arcuate-anastomosate, minor veins forming lax and more or less prominent reticulum.

Inflorescences axillary, cymose-paniculate, much shorter than leaves, peduncle erect, striolate, little compressed, pubescent-hirtellous, up to 3 cm. long, branches short, alternate (rarely dichotomous), angulate, hirtellous-puberulous. Bracts ovate or ovate-oblong, obtuse, amplexant, more or less puberulous, ciliate at margin, 2-0.5 mm. long. Ultimate branchlets short, hirtellous, 1-2 mm. long with 2-3 flowers. Pedicels very short (0.2-0.3 mm. long). Sepals thick, rounded, 1-1.2 mm. long, 1.2-1.5 mm. broad, puberulous, margin ciliate and with minute gland at apex. Petals thick, yellowish white, oblong, attenuate at apex, acute, 4.5-5 mm. long, 1.5 mm. broad, more or less

puberulous, estivation quincuncial. Stamens 20, uniseriate, glabrous, filaments united in tube at base, 5 episealous longer (2.5 mm.) shortly trifurcate and triantheriferous, medial anther larger and fertile, lateral anthers sterile, 5 epipetalous filaments (2 mm. long) and 10 alternating and shorter ones (1.5 mm.) entire and monantheriferous. Anthers dorsifixed, glabrous, 2 thecae basal, ellipsoid, unilocular, connective thick, ovoid, interiorly carinate, apex acute. Disk membranous, cupular, 0.8 mm. high, girdling ovary, margin about 20-dentate. Ovary globose, glabrous, 5-locular, 5-ovulate. Style 0.4 mm. long. Stigma capitate, 5-lobate. Ovule oblong-ellipsoid, anatropous with ventral raphe. Drupe globose, 3–4.5 cm. diameter, exocarp nearly smooth, coriaceous when dry, 3–5 mm. thick. Endocarp globose, hard, woody, almost smooth, copiously filled with resinous cavities, 2.6–3.4 cm. diameter, usually with 2 oblong seeds.

S. retusum differs from *S. reticulatum* essentially in its elliptic, broader, obtuse, sessile, or subsessile leaves with rounded base. The very short petiole or base of the midrib is much thickened and rounded; contrarily *S. reticulatum* has a very apparent and flattened petiole. The leaf blades are thicker in *S. retusum* and more attenuate and acute in *S. reticulatum*. The nerves are immersed and less conspicuous in the type of *S. retusum*, but in other specimens that undoubtedly belong to the species, they are more or less prominent.

S. retusum usually is a small tree found on sandstone elevations or sandy soils in the upper Rio Negro and Vaupés basins.

COLOMBIA: VAUPÉS: Cerro de Circasia, 300–400 m. alt., árbol, frutos grandes, comestibles, 10–X–1939, *Cuatrecasas* 7203 (COL; US, frag.). Riberas del Río Inírida; Raudal Guacamayo, margen izquierda, 180 m.; arbusto 3 m., inflorescencias péndulas, frutos péndulos, 4–II–1953, *Fernández* 2142 (COL, US).

BRAZIL: AMAZONAS: Rio Içana, Santana, caatinga aberta, terreno humido, arenoso; arbusto formando touças, frutos comestíveis, 18–XI–1945, *Fróes* 21411 (IAN, K, NY). Rio Içana, Santana, caatinga, arvore pequena, 2–V–1948, *Black* 48–2514 (IAN, NY, U, US, VEN). Rio Curicuriary, afluente Rio Negro super cataractem Cajú ad ripas; arbor submedia, 22–II–1936, *Ducke* 30131 (US, isotypes). Rio Preto, Campina, tree 25 ft. 7 in., white-yellow flowers, open campina, rather grassy country, sandy soil, 5–XI–1947, *Fróes* 22747 (IAN).

5. *Schistostemon macrophyllum* (Benth.) Cuatr., comb. nov.

FIGURES 31,*a–c*; 33,*a–b*; PLATE 18

Humirium macrophyllum Benth. in Hook. Journ. Bot. Kew Misc. 5:102. 1853.

Sacoglottis macrophylla (Benth.) Urb. in Mart. Fl. Bras. 12(2):446. 1877.—

Ducke, Arch. Jard. Bot. Rio Janeiro 6:40. 1933; Arch. Inst. Biol. Veget. Rio Janeiro 4:26, 29. 1937.

Sacoglottis Duckei Huber, Bul. Mus. Goeldi 5:413. 1909.—Ducke, Arch. Jard. Bot. Rio Janeiro 5:143, pl. 15, fig. 37. 1922.

Type: *Spruce*, Brazil, Amazonas, Barra do Rio Negro.

Small tree with greenish-brown, lenticellate, glabrous branchlets. Leaves firmly coriaceous, glabrous. Petiole 8–14 mm. long, semi-

terete, flat above, thickened at base. Blade ovate-oblong, rounded at base, attenuate and acuminate at apex, slightly crenulate at margin, 8–20 cm. long, 3.5–7.5 cm. broad; lustrous above with broad and slightly prominent midrib, secondary nerves and reticulum sharply prominulous; prominent striolate midrib beneath, 10–12 pairs of secondary nerves obscure-prominent, subascendent, more or less evanescent near margin, veins subimmersed, slightly conspicuous or obsolete, small punctiform glands along margin.

Inflorescence cymose-paniculate, axillary, much shorter than leaves, peduncle stout, compressed, short-pubescent, 1–3 cm. long, bifurcate; branches short, alternate, pubescent. Bracts coriaceous, persistent, ovate-triangular, rather obtuse, amplexant, carinate, glabrous but ciliate margin. Pedicels thick, very short (about 0.3 mm. long). Sepals thick, broad, orbicular, imbricate, about 1.5 mm. long, ciliate, glabrous without. Petals thick, greenish, glabrous, oblong, obtusish or subacute, 4.5–5 mm. long, 1.5–1.8 mm. broad. Stamens 20, glabrous, filaments compressed, lower half conerescent in tube, 2.5–4 mm. long, 5 longer trifurcate and triantheriferous. Anthers ovoid or rhomboid, about 1 mm. long with elliptic-oblong thecae about 0.5 mm. long, connective thick, angulate, subdeltoid-lanceolate. Sometimes sterile filaments found between the stamens. Disk annular-cupular girdling ovary, formed by 10 bidentate, connate scales, about 0.6–0.7 mm. long. Ovary subglobose, about 1.2 mm. high, glabrous, 5-locular, with uniovulate cells. Ovules oblong, about 1 mm. long. Style columnar, glabrous, 0.8 mm. long. Stigma capitate, 5-lobate. Drupe subovoid or oblong-ovoid, subrounded at base, abruptly attenuate at apex, subobtuse or shortly apiculate, smooth, 3.5–4 cm. long, 2–2.8 cm. broad, exocarp carnose (dry coriaceous), thin, endocarp woody, rather smooth or slightly bullate, with abundant spherical, resinous cavities.

S. macrophyllum is a frequent small tree on the flooded river margins of the Manaos and middle Rio Negro regions.

BRAZIL: AMAZONAS: Manaos, Rio Tarumá, igapó, arvore pequena, flor verde, 12–VIII–1942, *Ducke* 255 (A, IAN, MG, NY, S, US). Rio Tarumá, arvore 7 m. pendendo para o Rio, flores verde-brancas, 6–VIII–1949, *Fróes* 24916 (IAN); margen do rio, solo de areia, arvore de 5 m., 26–II–1950, *Fróes* 26071 (IAN). Margem do Igarapé do Tarumá; Igapó de agua preta, arbusto de 3 m., flor esverdeada, 22–VI–1955, *INPA*–1243 (MG–21545). Igarapé de Cachoeira Alta de Tarumá, arvore 8 m., flor esverdeada, 25–VIII–1954, *INPA* 244 (MG–21552). In ripis inundatis Igarapé da Cachoeira Grande, arbor parva floribus viridibus vix odoratis, 7–V–1933, *Ducke* 23816 (US, U); margem inundada, arvore pequena, 17–I–1943, *Ducke* 1175 (IAN, MG, NY, US). Igarapé do Cachoeira Grande dos Bilhares, terreno firme arenoso, capoeira, flor esverdeada, estames amarelos, arvore 6 m., caule tortuoso e muito esgalhado, 26–IX–1955, *INPA* 2044 (MG–21540); arbusto 3 m., 12–XII–1955, *Chagas* 3093 (IAN). Igapó do

Tarumazinho, agua preta, arvore caule tortuoso, 15-VII-1955, *INPA* 1407 (MG-21544). Manaos, silva paludosa, arbor floribus albidis, 26-VIII-23, *Kuhlmann* 21029 (US, S, U); silva paludosa, *Ducke* 21024, isotype of *Sacoglottis duckei* Huber, photo F.M. 12596. Manaos, praia baixa do Rio Negro, arvore pequena, flor verde, 1-IX-1945, *Ducke* 1744 (GH, IAN, MG, NY, US). Baixo Rio Negro, Tanacoera, praia, 26-IV-1911, *Ducke* 11550 (MG). Rio Negro, Padauiry, Tapera, tree 30 ft., yellowish white, flowers border of river of whitish water, low land, high forest, 11-X-1947, *Fróes* 22703 (IAN, NY, US, U). Rio Negro, Barcellos, Beira de uma ilha no rio, 23-VI-1905, *Ducke* 7174 (MG, holotype of *S. Duckei* Huber). Middle Rio Negro, Barcellos, flood bank, bush, flowers pinkish, 26-IX-14-X-1947, *Schultes & López* 8881 (IAN, US). Rio Negro, Tauapecaçu, shrub 20 ft. growing in clumps, yellowish flowers, border of rivers, sandy soil, *Fróes* 22472 (IAN); ad ripas inundatas fluminis Apuahú inferioris, arbor parva, floribus viridibus odoratis, 25-VII-1929, *Ducke* 23432 (S, US). Margen do Igarapé do Franco, arvore 5 m., frutos esverdeados, terreno arenoso, terra unida capoeira fechada, 20-II-1956, *Chagas & Dionisio* 3472 (IAN). Itaubal, Rio Aracá, subafuente do Rio Negro, caatinga, 26-X-1952, *Fróes & Addison* 29119 (IAN). Prope Barra, "prov. Rio Negro," VII-1851, *Spruce* 1714 (M, isotype). Mouth of Rio Negro, Igarapé da Colonia at Loge, 21-VII-1874, flowers yellowish, *Traill* 81 (K).

6. *Schistostemon dichotomum* (Urban) Cuatr., comb. nov. FIGURE 33,c-d

Sacoglottis dichotoma Urb. in Mart. Fl. Bras. 12(2):446. 1877.

Type: *Kappler* 2144, Surinam, Lava.

Tree with light-brown lenticellate terminal branchlets. Leaves coriaceous, rigid, glabrous. Petiole thick, semiterete, 6-12 mm. long, flat above, thickened at base. Blades oblong-ovate or ovate-elliptic, rounded or somewhat cuneate-decurrent at base, attenuate at apex, more or less cuspidate, margin slightly crenulate, 10-16 cm. long, 4-8 cm. broad; lustrous above with almost flat midrib, secondary nerves filiform and prominent; rather dull beneath with prominent striolate midrib, 8-10 pairs of secondary nerves slender, prominent subascendent, curvate and anastomosate with minute impressed distant glands near margin; minute vein reticulation sharply prominent and very conspicuous on both sides.

Inflorescences cymose-paniculate, dichotomous, axillary, half as long as leaves, peduncle slightly compressed, minutely puberulous, 3.5-6 cm. long, branchlets minutely pubescent, bracts amplexant, ovate, obtuse, 1.5-0.5 mm. long, short-ciliolate, persistent. Pedicels thick, up to 0.5 mm. long. Sepals rather thick, imbricate, suborbicular, glabrous except the minutely ciliate margin, 1 mm. long. Petals submembranaceous, yellowish, oblong, acute, glabrous, 3-3.5 mm. long, about 1 mm. wide. Stamens 20, glabrous, filaments complanate, lower part connate, 2.2-3.3 mm. long, 5 longer shortly trifurcate and triantheriferous at apex. Anthers ovate-rhomboid, about 0.9 mm. long, thecae ellipsoid-oblong, 0.4-0.5 mm. long, connective thick, angulate, ovate-lanceolate. Disk cupular, circling ovary, formed by 10 bidentate loose scales, 0.5-0.6 mm. long. Ovary

globose, glabrous, 0.8 mm. high, 5-locular, 5-ovulate. Style rather thick, about 0.6 mm. long. Stigma capitate 5-lobulate.

S. dichotomum is only known from the region bordering Surinam and French Guiana.

SURINAM: Ad fluvium Lava, arbor floribus flavis, October, *Kappler* 2144 (P, isotype). Marowijne River, 1861 (1862 ?), *Kappler* s.n. (U). Fluvium Lawa, prope Cottica, X-1903, *Versteeg* 265 (U).

FRENCH GUIANA: Maroni, "M. le Dr. Rech, 1862" (P). Collector unknown, "Guyane française" (P).

7. *Schistostemon densiflorum* (Benth.) Cuatr., comb. nov.

FIGURES 31,*d-f*; 33,*e-g*; PLATE 19

Humirium densiflorum Benth. in Hook. London Journ. Bot. 2:347. 1843.

Sacoglottis densiflora (Benth.) Urb. in Mart. Fl. Bras. 12(2):445. 1877.

Sacoglottis kaboeriensis Bakh. v.d. Brink f. apud Pulle in Rec. Trav. Bot. Neerl. 37:292. 1940.—Medel. Bot. Mus. Herb. Rijks Univ. 79:292. 1940.—Pulle, Flora of Suriname 3(1):420. 1941.

Type: *Schomburgk* 543, British Guiana, Quitaro river.

Medium-size tree with terete, more or less lenticellate, glabrous branchlets. Leaves coriaceous, more or less rigid, glabrous. Petiole 5–12 mm. long, semiterete, thickened at base. Blade ovate or ovate-oblong, rounded at base, narrowed, subacute or shortly acuminate at apex, margin slightly and distantly crenate, 7–19 cm. long, 3–7.5 cm. broad; lustrous above with flattened but conspicuous midrib and prominulous secondary nerves and reticulum; lustrous beneath with thick and prominent midrib, secondary nerves 10 pairs, prominulous, arcuate-ascendent, anastomosate near margin, veins forming minute prominent reticulum.

Inflorescences cymose-paniculate, axillary, dichotomous, alternate at the end, peduncle robust, slightly compressed, minutely pubescent, 1.5–3 cm. long, branchlets rather thick, pubescent. Bracts persistent, amplexant, 1.5–0.5 mm. long, ovate-lanceolate or sublanceolate, ciliate and more or less puberulous. Pedicels very short (0.1–0.3 mm.). Sepals ovate-orbicular, united at base, 0.7–0.8 mm. long, hispidulous-pubescent, ciliate at margin. Petals linear, attenuate at apex, 3.5–4.5 mm. long, 1 mm. broad, hispidulous-pubescent with retroflexed hairs. Stamens 20, glabrous, filaments united in lower half, complanate, 2–3 mm. long, 5 longer short trifurcate at apex, triantheriferous, others simple, acute, monantheriferous. Anthers ovoid, about 0.7 mm. long, thecae ellipsoid, connective carnose, lanceolate. Disk membranaceous, annular, 0.4 mm. high, dentate at margin. Ovary glabrous, ovoid, about 1.2 mm. high, 5-locular, cells uni-ovulate. Style about 1 mm. long. Stigma 5-lobate. Drupe ovoid-ellipsoid, about 2.6 cm. long, 2.3 cm. diameter, exocarp almost smooth, coriaceous when dry, 1.5–2 mm. thick. Endocarp ellipsoid, slightly

bullate, 2–2.3 cm. long, 1.8–2.2 cm. diameter, woody, resinous-lacunose, usually with one seed.

The type of *Sacoglottis kaboeriensis* can be distinguished from the typical *Schistostemon densiflorum* only by its larger and more flexible leaves; undoubtedly it only represents a form of younger plants from a more humid and shady habitat.

S. densiflorum is a tree growing mainly in the British and Dutch Guiana forests at the margin of the rivers.

BRITISH GUIANA: "In Guiana," *Schomburgk* 543 (isotype US, P). Esse-
quibo River, bank near Bartica, small tree, flower pale green; 5 petals, 10–15
stamens cohering below, 4–X–1929, *Sandwith*, 374 (NY, U). Bartica, XI–1888,
Jenman 4719 (NY); *Jenman* 2489, IX–1886 (BM). Comaka, Demerara River,
river bank, V–1923, *Persaud* 288 (F). Ruri, forest, clay soil, near Blue Moun-
tain, tree, VIII–1924, *Persaud* 102 (F, NY). Corantyne River, medium-size tree,
XI–1879, *Jenman* 287 (P); X–1879, *Jenman* 478 (P). County Berbice, Couran-
tyne River between Mapenna and Hubudikuru Creeks, 13–V–1918, "bukuria"
(Arawak), *Forest Department (Hohenkerk)* 404A (K). "British Guyana," VII–
1879, *Thurn* s.n. (K).

SURINAM: Corantyne River, Kaboerie, tree J.W.G. No. 138, 26–VI–1916,
Boschwezen 2068 (U, holotype of *Sacoglottis kaboeriensis*); tree 708, 30–II–1920,
Boschwezen 4933 (U); tree 593, 1–X–1920, *Boschwezen* 4960 (U).

8. *Sacoglottis*

Sacoglottis Mart., Nov. Gen. et Sp. Pl. 2:146. 1827.—Benth. in Hook. Journ.
Bot. Kew Miscel. 5:98, 103–104. 1853.—Benth. & Hook. Gen. Pl. 1:247
1862.—Muell. in Walp. Ann. Bot. Syst. 4:385. 1857.—Hemsl. in Hook.
Icon. Pl. 4 ser. 6:Pl.2521. 1897.—Lemée, Dic. Descr. Synon. Gen. Phan.
5:919 (in parte). 1934.—Bakhuizen van den Brink in Pulle Fl. Surin.
8(1):417. 1941.

Sacoglottis Sect. *Eusaccoglottis* (Urban), Winkl. in Engl. & Harms, Pflanzenfam.
19a:128, figs. 58, 59. 1931.

Saccoglottis Endl. Gen. Pl.:1040. 1840.—Baill. Adansonia 1:208. 1860;
2:265. 1861.—Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 4:28–29. 1937
(in parte).—Walp. Rep. Bot. Syst. 1:425. 1842.—Hutchinson & Daziel,
Fl. West Trop. Afr. 1:274 fig. 114. 1928.

Saccoglottis Subgen. *Eusaccoglottis* Urb. in Mart. Fl. Bras. 12(2):442, 448,
pls. 94–I, 95. 1877.

Saccoglottis Sect. *Eusaccoglottis* (Urb.), Reiche in Engl. & Prantl, Pflanzenfam.
3(4):37, fig. 32. 1890.

Houmiri Sect. *Aubrya* (Baill.), Baill. Adansonia 10:370. 1873.—Hist.
Pl. 5:54. 1874.

Houmiri Sect. *Saccoglottis* (Mart.), Baill. Adansonia 10:370. 1873.—Hist.
Pl. 5:54. 1874.

Aubrya Baill., Adansonia 2:265. 1862.—Oliver, Fl. Trop. Afr. 1:275. 1868.

Type species: *Sacoglottis amazonica* Martius.

Sepals 5, suborbicular, imbricate in estivation more or less united
at base. Petals 5, free, thick-membranaceous, estivation cochlear

or quincuncial. Stamens 10, glabrous, 5 opposite sepals longer than alternate ones, filaments thick, complanate, oblong-lanceolate, united at base. Anthers ovoid or ovoid-oblong, attached dorsally near base, thecae 2, unilocular, ellipsoid, affixed at lower side, dehiscing by detachment, connective ovate-acuminate, acute. Disk cupular, dentate, girdling ovary. Ovary 5-locular, cells uniovulate, carpels opposite sepals. Ovules anatropous with ventral raphe, pendulous. Style as long as or exceeding stamens. Stigma capitate and 5-lobate. Drupe of medium or large size, smooth, exocarp carnose, subcoriaceous when dry. Endocarp woody, more or less bullate, globose, filled with resinous cavities and commonly bearing only 1-2 oblong seeds. Evergreen trees with simple, alternate, coriaceous or subcoriaceous, petiolate leaves, with crenate or entire margin. Stipules small, deciduous or lacking. Inflorescences axillary or subterminal, paniculate with dichotomous or trichotomous branching. Bracts persistent or deciduous. Endocarp woody, more or less bullate with 10 very narrow, usually slightly apparent furrows; filled with globose, resinous, vacuous cavities; 5 septa in transection irregular and more or less conspicuous; commonly only 1 or 2 oblong seeds developed; apparently indehiscent but at germination developing embryos push off broad, thick, oblong-elliptic valves; these valves go almost from apex to base and have width of two stripes (between every third furrow); separating ribs being so thin that valves seem to cover whole surface of endocarp; germinal foramina at apex very rare. (See also figs. 1, 3, and 35-36.)

Sacoglottis has been spelled by Endlicher and others as "Saccoglottis," but the original spelling by Martius is with one "c." Sprague writes: "The generic name seems to have been derived from *σάκος* (sakos), more usually spelled *σάκκος* (sakkos) a sack, and *γλωττις* (glottis) a little tongue in allusion to the tonguelike connective separating the two thecae of the anther. There was therefore no orthographic error in the name *Sacoglottis*, and it must stand as published by Martius" (Sprague, 1929).

The genus *Sacoglottis*, as here understood, comprises eight species and several varieties and forms, which are spread widely throughout tropical South America from east of the Andes to the Atlantic coast; one species also is found on the Pacific drainage of Colombia and Costa Rica, and another reaches the Atlantic side of this Central American country. The southern limit in South America is in Rio de Janeiro. *S. gabonensis* is the only extra-American species of the family, and is found in tropical West Africa.

Key to the Species of *Sacoglottis*

1. Bracts deciduous.
 2. Leaves small, blades up to 3.5–3 cm. long, obovate, firm-coriaceous, smooth above, secondary nerves scarcely more conspicuous than minute, prominulous reticulum beneath. Petals hispidulous outside. Sepals hispidulous-pubescent. **1. *S. maguirei***
 2. Leaves larger, blades 6–22 cm. long, secondary nerves prominent and veins lax-reticulate, prominulous beneath.
 3. Drupe narrowly oblong, acute or apiculate, 4–5 cm. long, 1.3–1.8 cm. diameter. Inflorescence sessile or subsessile, conglomerate. Calyx broadly cupular. Petals glabrous. Leaves rigid-coriaceous.
 2. ***S. ceratocarpa***
 3. Drupe ovoid, ellipsoid or subglobose. Inflorescences conspicuously pedunculate.
 4. Leaves rigid-coriaceous, rather thick, sharply nerved beneath. Drupe ovoid, 5–5.5×4–4.5 cm., dry exocarp 6–7 mm. thick.
 3. ***S. ovicarpa***
 4. Leaves thin-coriaceous, flexible. Drupe ellipsoid or subglobose, dry exocarp 1.5–2.5 mm. thick.
 5. Sepals glandular at margin. Drupe oblong-ellipsoid, 5–6×3–3.5 cm. Petals glabrous, 4–4.5×1 mm. subobtuse. Filaments united for lower third. Disk dentate **4. *S. amazonica***
 5. Sepals not glandular or with very minute, scarce glands at margin. Drupe globose-ellipsoid, 2.7–3.5×2.5–3 cm. Petals pubescent outside, 6–7×1.5–2 mm., acute. Filaments united briefly at base. Disk fimbriate **5. *S. gabonensis***
 1. Bracts persistent.
 6. Drupe oblong, narrowed at base, acute or subobtuse at apex, 1.5–3 cm. long, 0.9–1.2 cm. thick. Leaves rigid-coriaceous, with immersed or slightly conspicuous nerves above and more or less conspicuously minute-reticulate beneath **6. *S. guianensis***
 6. Drupe spheroid or subspheroid.
 7. Drupe 1.7–2.8 cm. diameter; exocarp simple, compact, coriaceous, resinous-granulose, 1–2 mm. thick; endocarp rather smooth, slightly bullate and forrowed. Leaves thin-coriaceous, flexible, prominently lax-reticulate both sides **7. *S. mattogrossensis***
 7. Drupe 1.5–2 cm. diameter; exocarp 3–5 mm. thick, double, outer layer coriaceous, compact, resinous-granulose, inner part densely fibrous; endocarp more or less tuberculate. Leaves rigid-coriaceous, with slightly or not conspicuous nerves above and prominulous, minute reticulum beneath **8. *S. cydonioides***

1. *Sacoglottis maguirei* Cuatr., sp. nov.

FIGURE 34, f

Arbor parva, ramulis ultimis brunnescentibus lenticellatis minutissime hirtulis.

Folia rigida coriacea petiolo 3–6 mm. longo supra canaliculato subtus semitereti basi incrassato, minute hirtulo-puberulo. Lamina obovata apice subtruncata vel subrotundata vel obtusissima basi subite cuneata margine 4–6 dentibus obtusis distantibus utroque latere, 2–3.5 cm. longa 1.5–3 cm. lata; supra nitida laevis tantum costa

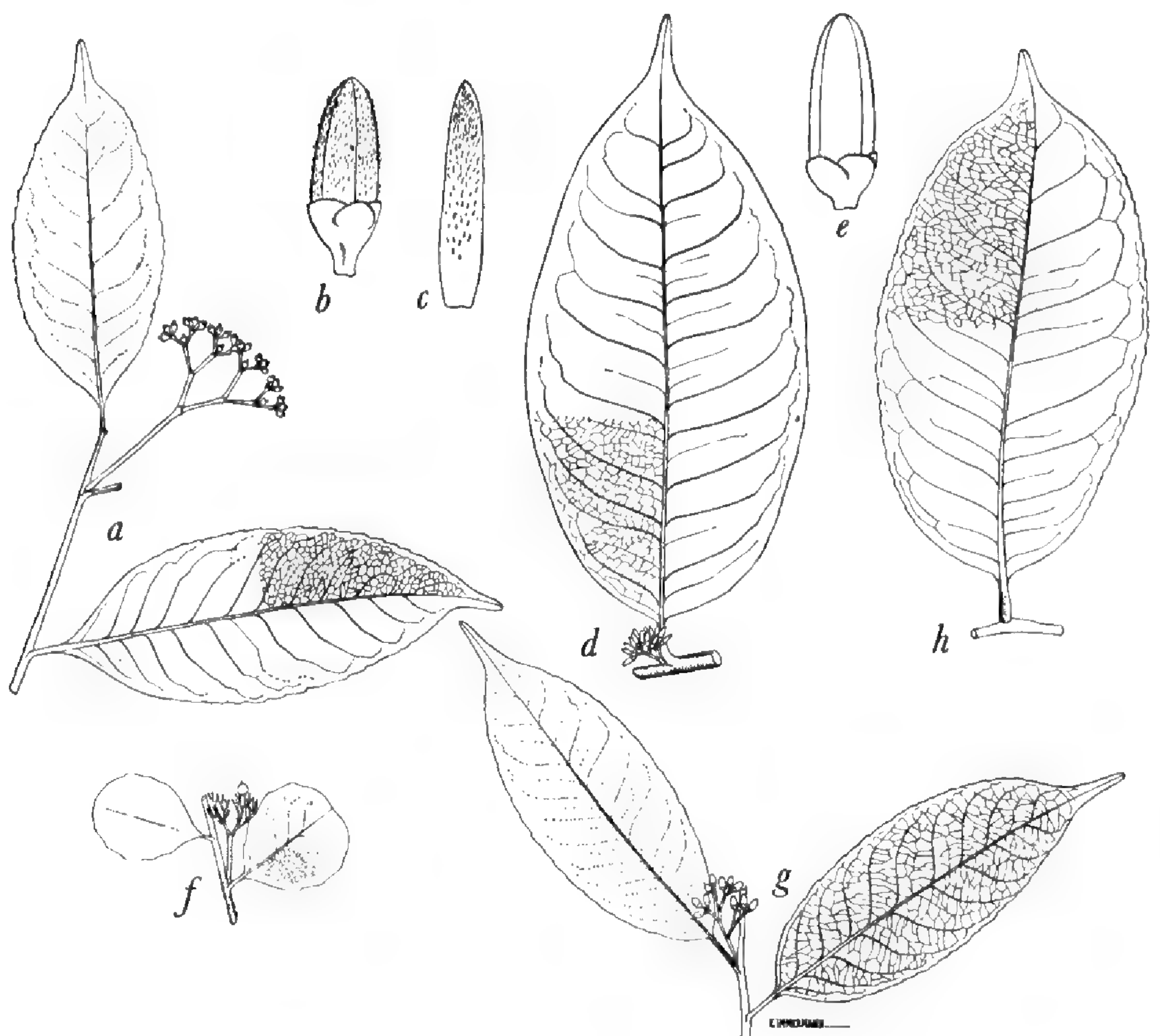


FIGURE 34.—*a-c*, *Sagoglottis gabonensis* (Koechlin 2632): *a*, terminal branchlet, $\times \frac{1}{3}$; *b*, bud, $\times 3\frac{1}{3}$; *c*, petal $\times 3\frac{1}{3}$; *d-e*, *Sacoglottis ceratocarpa*: *d*, $\times \frac{1}{2}$ (Fréès 21192); *e*, bud, $\times 3\frac{1}{3}$ (Ducke 12); *f*, *Sacoglottis maguirei*, $\times \frac{1}{3}$ (Maguire et al. 30693); *g*, *Sacoglottis amazonica*, $\times \frac{1}{3}$ (Ducke 1723); *h*, *Sacoglottis ovicarpa*, $\times \frac{1}{3}$ (Cuatr. 19998).

conspicua; subtus subnitida costa prominenti, nervis secundariis paulo distinctis nervulis minutum reticulum prominulum formantibus.

Inflorescentiae axillares foliis breviores, pedunculo 0.8–1.5 cm. longo, robusto striato minute hirtello, ramis inferne dichotomis brevibus ultimis fertilibus 2–4 mm. longis erectis minute hirtulis. Bractae deciduae. Sepala rotundata 0.5 mm. longa (in alabastro 1.5 mm. longo), pubescenti-hispidula. Petala oblonga subacuta extus hispidula, 1.3 mm. longa (in alabastro). Stamina 10 filamentis glabris complanatis triangularibus, margine papillosis dimidia parte inferiori coalitis, brevibus 1.2 mm. longis cum longioribus 1.6 mm. longis alternantibus. Antherae oblongae 0.5 mm. longae thecis oblongis, connectivo crasso apice obtusiusculo. Ovarium glabrum. Stylus 0.4 mm. longus. Stigma capitatum 5-lobatum. Fructus satis juvenilis tantum vidi subglobosus glabrus numerosis cavitatis resinosi instructus.

The small, rigid, broadly dentate leaves of *S. maguirei* are different from the leaves of all other species of the genus. This species is

xeromorphic, adjusted to the ecologic conditions of the high Guiana plateaus.

Type in the U.S. National Herbarium, No. 2270195, collected at Mount Cerro Yapacana, where it is frequent in cumbre, at an altitude of 1,200 m., Orinoco River region, State of Amazonas, Venezuela, January 3, 1951, by Bassett Maguire, Richard S. Cowan, and John J. Wurdack (No. 30693). Isotype in the Herbarium of the New York Botanical Garden.

Small tree with brownish, lenticellate, minutely hirtellous terminal branches. Leaves small, coriaceous, rigid. Petiole 3–6 mm. long, sulcate above, semiterete below, thickened at base. Blade obovate, subtruncate, subrotundate or obtuse at apex, abruptly cuneate at base, distantly and obtusely dentate at margin, 2–3.5 cm. long, 1.5–3 cm. broad; lustrous, smooth with only midrib conspicuous above; less nitid beneath with prominent midrib, secondary nerves little distinct and veins forming minute and prominulous reticulum.

Inflorescences axillary, shorter than leaves, peduncle 0.8–1.5 cm. long, stout, striate, minutely hirtellous; branches dichotomous on first divisions, short, last ones fertile, 2–4 mm. long, erect and minutely hirtellous. Bracts deciduous. Sepals rounded, 0.5 mm. long (in buds 1.5 mm. long), pubescent-hispid. Petals oblong, subacute, hispidulous, in buds 1.3 mm. long. Stamens 10, filaments glabrous, complanate, triangular, papillose, lower half conrescent, 5 longer 1.6 mm. long alternating with 5 shorter 1.2 mm. long. Anthers oblong, 0.5 mm. long with oblong thecae and thick and subobtuse connective. Ovary glabrous. Style 0.4 mm. long. Stigma capitate 5-lobate. Drupe very young, subglobose, glabrous and with many resinous cavities.

VENEZUELA: AMAZONAS: Río Orinoco, Cerro Yapacana, alt. 1,200 m., Maguire, Cowan, & Wurdack 30693 (US, holotype; NY, isotype).

2. *Sacoglottis ceratocarpa* Ducke, Bol. Tec. Inst. Agr. Norte 4:13. 1945.
FIGURES 34, *d–e*; 35, *i–k*

Type: *Ducke* 12 and 1174, Brazil, Amazonas, Manaus.

Medium-size or small tree with hirtellous, soon glabrous, young branchlets. Leaves rigid, coriaceous, glabrous. Petiole 7–13 mm. long, robust, subterete, more or less winged, flat above, thickened at base. Blade ovate-oblong or ovate-elliptic-oblong, rounded or obtuse at base, attenuate and acuminate or cuspidate at apex, slightly crenate at margin; 8–22 cm. long, 3.5–10 cm. broad, brownish when dry; above smooth with almost flat midrib, secondary nerves and veins obsolete; beneath with prominent midrib, secondary nerves thin but prominent, 10–12 pairs, subspreading, near margin arcuate,

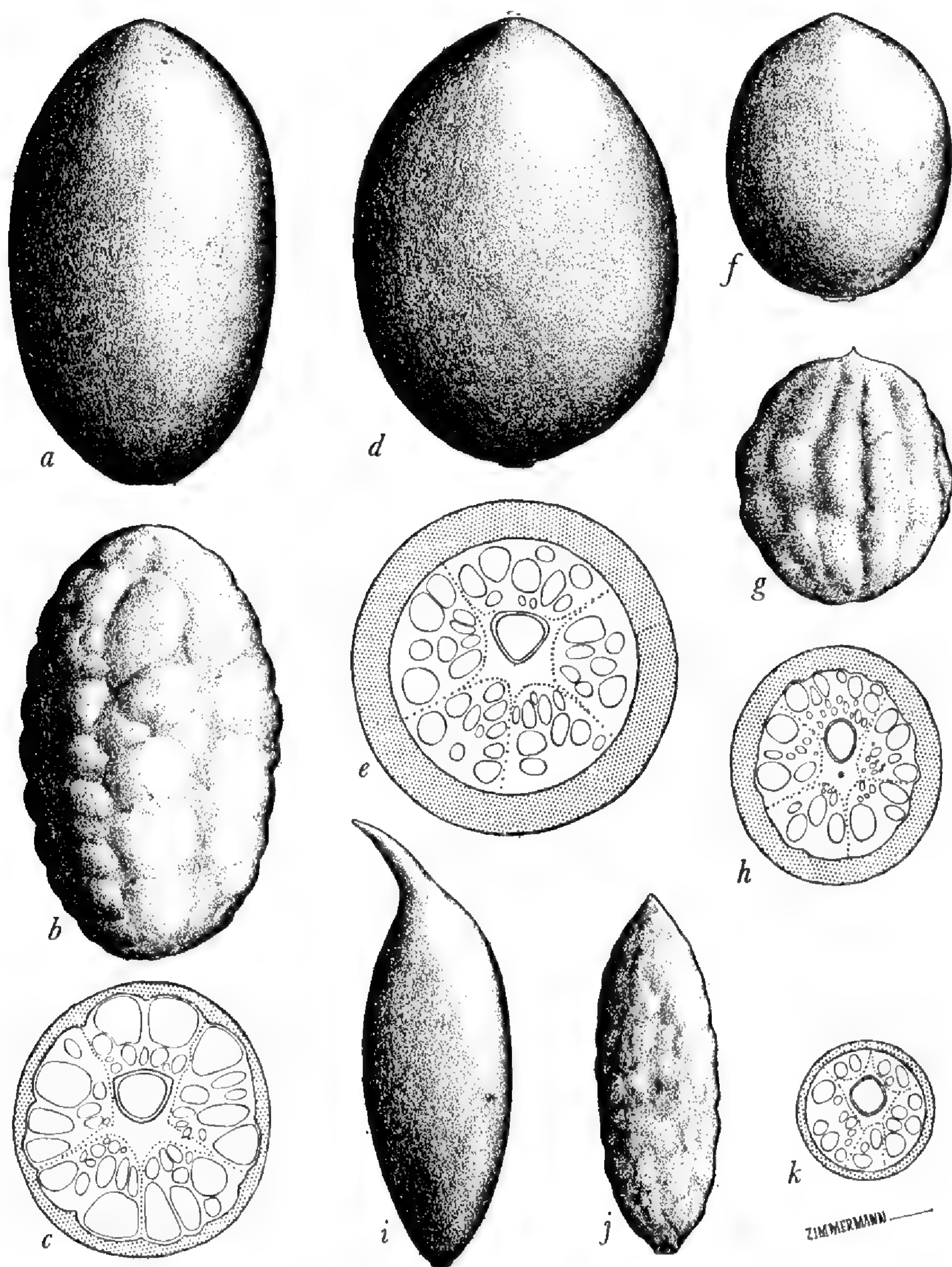


FIGURE 35.—*a-c*, *Sacoglottis amazonica*, $\times 1$ (Archer 7964): *a*, fruit; *b*, endocarp; *c*, transection. *d-e*, *Sacoglottis ovicarpa*, $\times 1$ (Cuatr. 19998): *d*, fruit; *e*, transection. *f-h*, *Sacoglottis gabonensis*, $\times 1$ (Krukoff 121): *f*, fruit; *g*, endocarp; *h*, transection. *i-k*, *Sacoglottis ceratocarpa*, $\times 1$ (Ducke 1174): *i*, fruit; *j*, endocarp; *k*, transection.

ascendent, anastomosate, minor veins forming a lax-prominulous reticulum.

Inflorescences axillary, cymose-paniculate, dichotomous, very short, sessile, subglomeriform; peduncle almost absent, branchlets reddish, angulate, short-pubescent, hirtellous. Bracts ovate-triangular, acute, subglabrous, 0.5–1 mm. long, deciduous. Pedicels very short articu-

late to very short peduncles. Sepals about 1.5 mm. long, rather thick, orbicular, imbricate, glabrous except for ciliate margin. Petals greenish, thick, glabrous, linear, subacute, about 5 mm. long, 1 mm. broad. Stamens 10, united in lower half, glabrous, filaments compressed, 2.5 and 3 mm. long alternating. Anthers ovoid-oblong, about 1.2 mm. long, thecae elliptic about 0.5 mm. long, connective thick, ovoid-sublanceolate, subacute. Disk membranaceous, denticulate ring 0.7–0.8 mm. high. Ovary ovoid, glabrous, 5-locular, cells uniovulate, attenuate at apex. Style 2–3 mm. long, erect, glabrous. Stigma capitate, 5-lobulate. Drupe elliptic-oblong-elongate, attenuate at both ends, subfusiform, apex acute, often apiculate, 4–5 cm. long, 1.3–1.8 cm. diameter, plus apiculum up to 8 mm. long. Exocarp smooth, subcoriaceous when dry, 1 mm. thick. Endocarp woody, narrowly oblong, acute at apex, resinous-lacunose, surface slightly bullate.

S. ceratocarpa is limited to the upper northern Amazon Basin. Its presently known range extends from the lower Colombian Vaupés region to the Manaus area.

A. Ducke wrote the following interesting remarks about the distribution of this species and its relation to *S. amazonica*: "This species has been confused with *S. amazonica* since the time of Martius who cited his *S. amazonica* not only for the Amazon estuary but also for the upper Amazon where this species probably does not exist (he certainly did not know the fruits of both species). The true *S. amazonica* grows rather frequently on the shores of streams subjected to the influence of the Atlantic tide; I observed it near Belém, on the Islands of Breves, and near Gurupá at the head of the Amazon estuary. Its fruit has a thin, more coriaceous than fleshy, mesocarp and is apt to float; old endocarps can be found every time on the banks of the rivers around the city of Pará. *S. ceratocarpa*, on the contrary, grows in the central part of Amazonia in marshy upland forest along streamlets, and its fruits do not seem apt for water transport, but they are probably dispersed by forest animals. Their white, more farinaceous than fleshy, mesocarp is somewhat like that of *S. heterocarpa* Ducke, growing in 'caatinga,' in the upper Rio Negro basin."

COLOMBIA: AMAZONAS-VAUPÉS: "Caño Oogö-'dja," Jinogojé, flowers white, tips orange, "nee-saw-kaw'-kě-too" (Makuna), 26–VIII–1952, *Schultes & Cabrera* 17045 (US). VAUPÉS: Between Mitú and Javaraté, Tipiaca, Igarapé Murutinga, small tree, 14–24–V–1953, *Schultes & Cabrera* 19290a (US). Río Piraparaná (tributary of Río Apaporis), Caño Teemeena, 6–IX–1952, bush, flowers yellowish, 6–IX–1952, *Schultes & Cabrera* 17253 (US). Río Paca (tributary of Río Papurí), Uacaricuari and vicinity, 650 ft., tree, flowers yellowish, 1–3–VI–1953, *Schultes & Cabrera* 19519 (US).

BRAZIL: AMAZONAS: Manaus, Pensador, silva paludosa secus rivulum; arbor mediocris fructibus maturis viridiflavis, "uchy-rana," 23–I–1943, *Ducke* 1174

(IAN, NY, US, isotypes; MG, holotype). Pensador, silva paludosa secus rivulum; arbor mediocris, floribus viridibus, "uchi-rana," 20-VIII-1935, *Ducke* 12 (isotype, florum, A, NY, S, US). Pensador, silva paludosa non inundabili secus rivulum; arbor mediocris floribus viridibus, "uchi-rana," 31-VII-1943, *Ducke* 1301 (IAN, MG, NY, US, A). Manaos, silva paludosa circa Cachoeira do Mindu, arbor media floribus viridibus, 15-VII-1929, *Ducke* 23431 (paratypes, US, U). Manaos, beira do Rio Tarumá, Igapo; arvore 5 m., flores verde-brancas, ramos pendentes, 7-VIII-1949, *Fróes* 24934 (IAN). Rio Tarumá, beira alagada perto da cachoeira baixa, arvore pequena, 11-I-1949, *Guedes* 80 (IAN, US); 25-VII-1948, *Guedes* 58 (IAN, US). Estrada do Tarumá, terreno arenoso, capoeira; flor esverdeada, arvore 7 m., caule ereto, 4-VIII-1955, *INPA* 2084 (MG 21539). Igarapé da Cachoeira do Tarumá, mata de varzea; flor amarelo esverdeada, 2-IX-1955, *INPA* 1814 (MG 21547). Manaos, Estrada da Forquilha, terra umida capoeira; arvore de caule tortuoso, flor verde, 12-VIII-1955, *INPA* 1638 (MG 21543). Silva non inundabili ad margines paludosas rivuli, arbor sat magna floribus viridibus, "uchi-rana," 31-VIII-1931, *Ducke* 16, *Ducke* 16a (Y). Rio Papury, Vaupés-Rio Negro, terra firme, terreno silicoso, arvore 20 m. 30 cm., 17-VIII-1945, *Froes* 21192 (NY, US, K, IAN).

3. *Sacoglottis ovicarpa* Cuatr. Trop. Woods 96:39. 1950.

FIGURES 34,h; 35,d-e

Type: *Cuatrecasas* 19998, Colombia, Valle, Buenaventura.

Large tree with 50 cm. thick trunk, rugose and dark bark that is reddish or pink in section, hard, yellowish pink wood, subterete and glabrous branchlets. Leaves coriaceous, glabrous, reddish brown when dry. Petiole subterete, 8-14 mm. long, robust, thickened toward base. Blade elliptic or ovate-elliptic, rounded or obtuse at base, abruptly narrowed and cuspidate at apex. Margin slightly crenulate, 9-16 cm. long, 3.5-9 cm. broad; above yellowish greenish, lustrous, with conspicuous midrib and inconspicuous lateral nerves and reticulum; beneath pale green, midrib prominent, the prominent lateral veins spreading distantly, 8-10 pairs, arcuate-anastomosate near margin, minor nerves conspicuously reticulate and prominulous. Drupe ovoid or ovoid-ellipsoid, approximately form and size of hen egg (5-5.5 × 4-4.5 cm.), greenish, nitid; exocarp carnose, hard and coriaceous when dry, 6-7 mm. thick; endocarp woody, almost smooth, irregularly 5-septate, abundantly provided with large rounded, nitid, resinous cavities; usually 1-2 seeds, rarely 5. Inflorescences and flowers unknown.

Collected by the author on the west coast of Colombia, *S. ovicarpa* is a large hardwood tree that probably grows along the entire Pacific coast in the uninundatable forest from Ecuador to Costa Rica. It replaces on this side of the continent the Atlantic large-fruited species *S. amazonica*, the Andean chains separating the two species. The Pittier specimens (16260) from the Cocos Islands on the Pacific coast of Costa Rica are almost sterile (they have only very young fruit), but I have almost no doubt that these specimens belong to this species. Likewise belonging to *S. ovicarpa* are the endocarps encoun-

tered by I. Johnston (1949, p. 52) among the drift deposits at the San José Island shores (Panama). These fruit, as suggested by Johnston, undoubtedly originated on the southern Pacific slopes (Panama to Ecuador) and drifted northward with the oceanic current. The fruit of *S. ovicarpa* differ from those of the very closely related *S. amazonica* by being ovoid and having a thicker and tougher exocarp; the endocarp has the irregularly distributed resinous cysts separated by thin walls, breakable at the surface, whereas in *S. amazonica* the resinous cysts are conspicuously arranged in 10 rows with thicker and stronger woody walls.

COSTA RICA: Cocos Island, Pacific, Le plus grand arbre de l'île; appelé "palo de hierro" par les colons; caractéristique pour les forêts, 10–250 m., I–1902, *Pittier* 16260 (US). The material is almost sterile including the leafy branchlets and a few initiations of fruit; more complete collections will be necessary to assure this identification.

COLOMBIA: EL VALLE: Costa del Pacífico, Bahía de Buenaventura, Quebrada de Aguadulce, 0–10 m. alt.; gran árbol, hoja coriácea, verde amarillenta oscura; fruto ovoide-elipsoideo, 5.5×4.5 cm., exocarpo carnoso-duro, verde brillante, 7–7 mm. grueso, endocarpo leñoso, "guayabito", 24–II–1946, *Cuatrecasas* 19998 (holotype F, isotype VALLE). Bahía de Buenaventura, Quebrada de San Joaquín, 0–10 m. alt.; gran árbol, tallo 45 cm. diám., corteza sublísa, pardo-rosada, en sección rosada o roja, en la base del tallo gris verdosa clara y separable; madera dura, amarillo-rosada; hoja coriácea rígida, dura, frágil, verde oscura brillante haz, verde claro envés, "corosillo," 22–II–1946, *Cuatrecasas* 19927 (F, VALLE). Río Cajambre, Barco, 5–80 m. Cerro El Sapote en el brazo del Río Agua Sucia; árbol 30 m., tallo 50 cm. diam., corteza rugosa, pardo-rojiza, sección rosada, zumosa; madera blanco-ocrácea, zumosa; frutos ovoideos, verdosos, carnoso-coriáceos, endocarpo semileñoso, 6×5 cm., "chanusillo," "chanosillo," "chanesillo," 28–IV–1944, *Cuatrecasas* 17226 (paratypes F, VALLE).

4. *Sacoglottis amazonica* Mart. Nov. Gen. Sp. Pl. 2:146. 1827; Fl. Bras. (12)2:449, tab. 95. 1877.—Ducke, Arch. Jard. Bot. Rio Janeiro 3:179. 1922; 5:142, pl. 14, fig. 36. 1930; Arch. Inst. Biol. Veget. Rio Janeiro 4:26 and 29. 1937.—Hemsl. in Hook. Icon. Pl. 4 ser., 6:Pl. 2521. 1897.

FIGURES 1,*d–f*; 34,*g*; 35,*a–c*; 36,*a–g*; PLATE 20

Type: *Martius*, Brazil, "Crescit in sylvis secus fluvium Amazonum et in ripa canalis Tagipuru."

Medium-size tree with glabrous young branchlets. Leaves thin-coriaceous, flexible, glabrous. Petiole 5–12 mm. long subterete, slightly winged, sulcate above, lower portion thickened. Blade oblong-elliptic sublanceolate, obtusely cuneate or very obtuse at base, narrowed toward apex and acuminate-cuspidate, slightly crenate at margin; 6–15 cm. long, 2.5–5.7 cm. broad, acumen about 1 cm. long; above with flat midrib, secondary nerves and veins when young more or less prominulous, later almost inconspicuous; beneath with eminent striolate midrib, secondary nerves, 9–12 pairs, thin but prominent, subpatulous, extreme ascendent, curvate-anastomosate, veins laxly reticulate, more or less prominent.

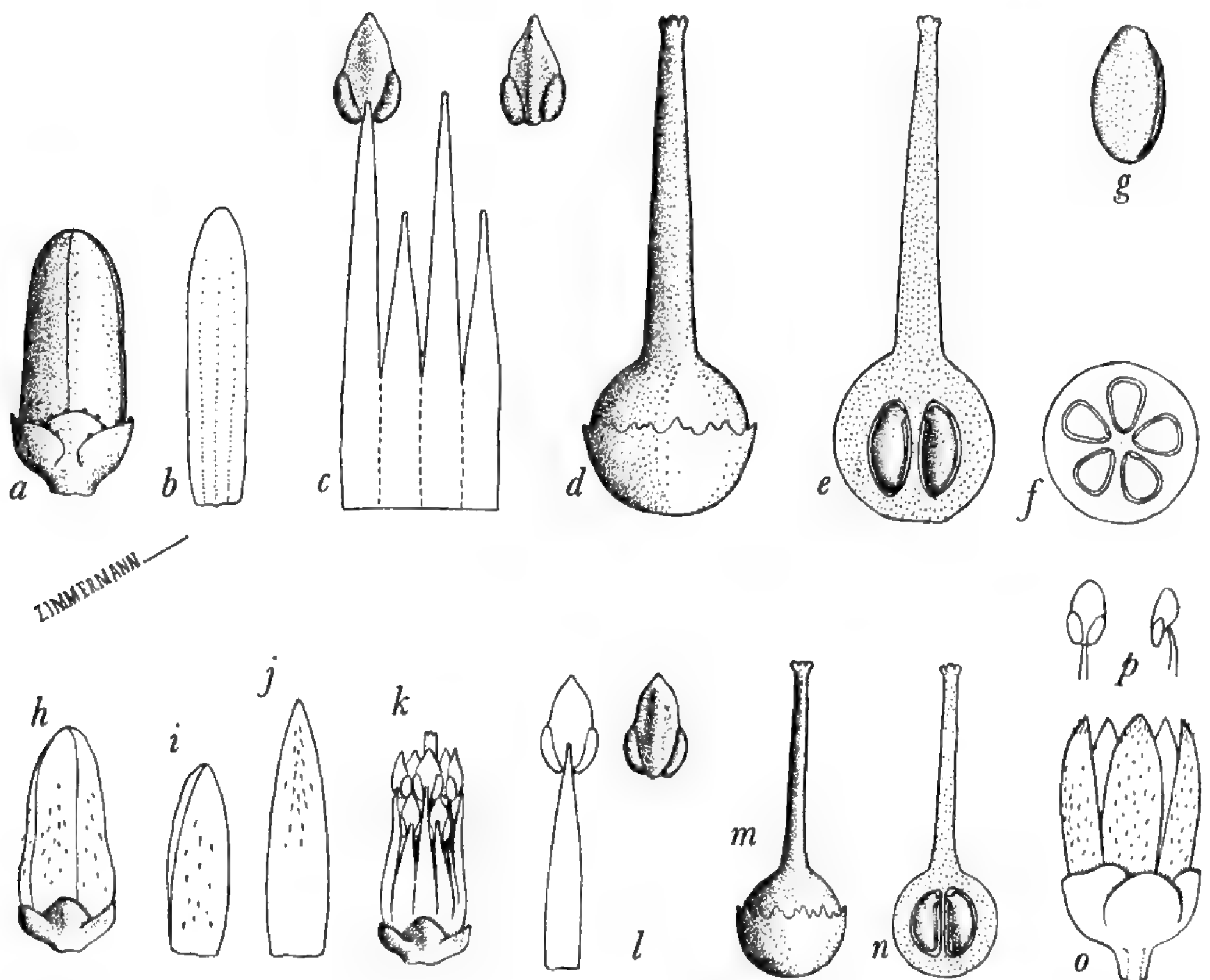


FIGURE 36.—*a-g*, *Sacoglottis amazonica* (Ducke 1723): *a*, bud, $\times 5$; *b*, petal, $\times 5$; *c*, detail of staminal tube from outside and one anther from inside, $\times 10$; *d*, gynoecium and disk, $\times 10$; *e*, longitudinal section of ovary; *f*, transection of ovary, $\times 10$; *g*, seed, $\times 20$. *h-n*, *Sacoglottis mattogrossensis* fma. *subintegra* (Ducke 23820): *h*, bud, $\times 5$; *i*, *j*, petals (more or less developed), $\times 5$; *k*, flower with petals removed $\times 5$; *l*, stamen dorsal view, and anther inner view, $\times 10$; *m*, gynoecium and disk, $\times 10$; *n*, gynoecium, longitudinal section. *o-p*, *Schistostemon auyantepuiense* (Vareschi & Foldats 4673): *o*, opening bud, $\times 5$; *p*, anthers, $\times 10$.

Inflorescences cymose-paniculate, axillary, much shorter than leaves, peduncle subterete, striate, glabrous, branchlets alternate, striolate, glabrous or upwardly sparsely pilose. Bracts deciduous, ovate-triangular, acute, about 1 mm. long. Pedicels short, thick, glabrous, often articulate to short (about 1 mm.) peduncles. Sepals 1–1.5 mm. long, broadly orbicular, imbricate, thickened, glabrous outside, margin minutely ciliate and with small glands. Petals linear-oblong, sub-obtuse, glabrous, about 4 mm. long, 1 mm. broad (at base 1.5 mm. broad), whitish-greenish. Stamens 10, glabrous, filaments complanate, smooth, lower third connate, 5 shorter 3 mm. long, lower ones about 4 mm. long. Anthers ovate-oblong, about 1 mm. long with half long thecae, connective thickened, angulate, sublanceolate. Disk girdling ovary, dentate, 0.6–0.7 mm. high. Ovary ovoid, about 1.5 mm. high, glabrous. Style 2.5–3 mm. long. Stigma capitate, 5-lobate. Drupe oblong-ellipsoid, 5–6 cm. long, 3–3.5 cm. diameter.

Exocarp more or less smooth, coriaceous when dry, 1.5–2 mm. thick. Endocarp slightly and irregularly 10-sulcate and bullate, woody, filled with resinous cavities, usually with only 1 oblong seed.

Sacoglottis amazonica varies from a large to a small tree present in flooded forests of the Amazon Basin, chiefly at its estuary. This species is also recorded from the Orinoco delta, from British and French Guiana, Trinidad, and some islands of the Lesser Antilles. Sterile collections from Costa Rica have foliage that agrees completely with the foliage of this species; however, I consider these collections as provisionally belonging to this species until flowering and fruiting material is made available.

The ellipsoid, 4–6 cm. long fruit (dark purplish according to Broadway) are a remarkable feature of *S. amazonica*; its endocarp filled with resinous, vacuous cavities is light and apt to float and be carried by the rivers and currents. Ducke states that endocarps are always on the banks of the rivers around the city of Pará. But these endocarps have also been found at many other places. Picked up by currents at the Amazon and Orinoco deltas, the endocarps have been drifted to the shores of the West Indies and Central America, and strangely enough even across the Atlantic Ocean to Great Britain.

The hardwood of *S. amazonica* is used in house construction. The most common name for the species is "uchi-rana" in Brazil, with some phonetic and spelling variants. In British Guiana it is called "funyu" and "nabaru" by the Guaraos of the Orinoco delta. According to Devenish the local name in Trinidad is "cojón de burro."

COSTA RICA: LIMÓN: Hills above La Florida, alt. 750 ft., rain forest, associated with "pejiballito," "pilón," "plomillo," "bernabé," volcanic loam, tree 60 ft., DBH 12 in., "campana," 7-V-1943, *Dayton & Barbour* 3004 (US, Y, 40838), sterile specimens. Hills 4 miles south of Sequirres, alt. 500 m., north slope, clay loam, rain forest tree 80 ft., DBH 28 in., usable length 40 ft., "campana," 7-V-1943, *Merker, Scholtes, & Dayton* 3041 (Y, 40842), sterile specimens. These identifications have to be considered provisional until fruit and flowering specimens from the same region are made available.

TRINIDAD: Palo Seco, washed upon beach, 20-III-1920, *Britton*, s.n. (NY). Irois, 28-XI-1916, *Broadway* 8475 (NY). Cedros, forest, 18-VIII-1896, *Lunt* s.n. (BM, US). Irois, VI-1896, *Lunt* 5984 (NY, K); *Hart* (NY).

ST. VINCENT: *L. Guilding* s.n. (K).

VENEZUELA: DELTA AMACURO: Antonio Diaz, Caño Jobure, occasionally in flooded forest along upper part; tree 15–20 m., buds greenish white; fruit green, edible, used by Guaraos for diarrhea treatment; "nabaru" (Guarauno); wood heavy used locally in heavy construction, 7-IV-1955, *Wurdack* 293 (NY, US, VEN).

BRITISH GUIANA: Rain forest on hilltop 8 miles east of Onoro Creek mouth, alt. 1000 ft., "funyu," 30-IX-1952, *Guppy* 308 (NY).

BRAZIL: PARÁ: Belém, silva inundata, arbor media floribus viridibus 24-VIII-1922, *Ducke* 17781 (S). Belém, *Pires & Black* 31 (P, U); south forest of the IAN, "achua-rana," 2-XII-1942, *Archer* 7915 (IAN, US); same place,

13-XII-1942, "uchyrana," *Archer* 7964 (IAN, US). Belém, Utinga, igapo, margen de riachos, 14-X-1916, *Ducke* 16578 (MG, US, U). Utinga, Igapo Buiussuquara; arbor parva floribus viridibus, "uchi-rana," 13-VII-1945, *Ducke* 1723 (A, IAN, MG, NY, US). Gurupa, margen de um riacho na varzea; arvore mediana, flor verde; "uchi-rana," 17-VIII-1918, *Ducke* s.n. (IAN); *Ducke* 17221 (BM, US, P, MG). Beira do Rio Guama, entre S. Miguel e Acary; arvore pequena; fruto perto d'agua 7 × 3 cm., verde, flor branca verdusca, 31-X-1948, "uchi-rana," *Black & Foster* 48-3393 (IAN). Beira do Rio Mapua, entre Vila Emilia e Boca do Mapua, varzea; arvore, flor branca, 18-VII-1950, *Black, Fróes, & Ledoux* 50-9810 (US). Rio Curupere, afluente do Rio Abaete, igapo, municipio de Abaetetuba; arvore, fruto verde, "uchirana", 19-IX-1952, *Araujo* 6 (IAN). Arama, beiro do rio, "uchi-rana," 26-II-1900, *Huber* 1850 (MG). Brasilia in itinere amazonico in ripa (canalis) Tagipuru, Obser. 2671, *Martius* s.n. (M, holotype; M, isotypes). AMAZONAS: Esperança (ad ostium fluminis Javary), silva non inundabili; arbor magna, floribus viridibus, 30-X-1942, *Ducke* 1055 (NY, MG, IAN, US). Municipio Humayta near Tres Casas, on low terra firma, tree 80 ft., 7-X-1934, *Krukoff* 6506 (GH, NY, U). Brasilia in sylvis ad Egam prov. Rio Negro, Dr. Martius iter Brasiliensium, *Martius* s.n. (M, paratypes).

5. ***Sacoglottis gabonensis*** (Baill.) Urb. in *Mart. Fl. Bras.* 12(2):449. 1877.—Reiche in *Engl. & Prantl, Pflanzenfam.* 3(4):37, fig. 32. 1890.—Winkler in *Engl. & Harms, Pflanzenfam.* 19a:128, fig. 58. 1931.—Hutchinson & Daziel, *Fl. West Trop. Afr.* 1:274, fig. 114. 1928.—Exell, *Journ. Bot.* 65 (Supl. Polypet.):50. 1927 (as *S. gabunensis*).—Guinea, E., *Ensayo geobotánico de la Guinea continental española*, 300. 1946.—Exell & Mendoça, *Conspectus Fl. Angolensis* 1:249. 1951.

FIGURES 34,a-c; 35,f-h

Aubrya gabonensis Baill. *Adansonia* 2:266. 1862.—Oliver, *Fl. Trop. Afr.* 1:275. 1868.

Houmiri gabonensis Baill. *Hist. Pl.* 5:52. 1874.

Aubrya occidentalis A. Chevalier, *Expl. Bot. Afr. Occident. Fr.* 1:94. 1920, nomen.

Type: *Aubry-le Compte*, Africa, Gabon.

Large tree with glabrous terminal branchlets. Leaves thin-coriaceous, flexible, glabrous. Petiole 6-10 mm. long, narrowly winged toward top, thickened at base. Blade ovate-elliptic or elliptic-oblong, suddenly and obtusely narrowed at base and slightly decurrent on petiole, narrowed-acuminate at apex, slightly crenate; 7-14 cm. long, 3-7 cm. broad; flat smooth midrib above, lateral nerves prominulous but little conspicuous; midrib beneath prominent, secondary nerves filiform, prominent, about 12 pairs, subpatulous, curvate-anastomosate near margin, veins rather lax-reticulate, prominulous.

Inflorescences cymose-paniculate, dichotomous, robust peduncle and branches minutely pubescent. Pedicels 0.5-1.5 mm. long, thick, angulate, puberulous or hirtellous-pubescent, articulate to short peduncle or sessile. Bracts amplexant, persistent, triangular, carinate, pubescent and ciliate, about 2 mm. long. Sepals 1.5 mm. long, broadly orbicular, imbricate, puberulous at base, ciliate at

margin. Petals thick, linear, subacute, subsericeous, 6–7 mm. long, 1.6–2 mm. broad. Stamens 10, filaments thickened, complanate, connate at base, 5 oppositipetalous oblong, subacute, about 3.5 mm. long, 0.5–0.6 mm. wide, alternating with 5 longer, linear, 4–5 mm. long, 0.3–0.4 mm. wide. Anthers with ellipsoid thecae about 0.6 mm. long, connective thick, lanceolate, compressed at upper part, those of shorter filaments 2 mm. long, those of longer ones 1.5 mm. long. Disk membranous, 0.8–1.5 mm. high, laciniate. Ovary ovoid, glabrous, 5-locular, cells opposite petals and uniovulate, about 2 mm. high. Style thick, erect, 3 mm. long. Drupe short-ellipsoid or subglobose, 2.7–3.5 cm. long, 2.5–3 cm. broad; exocarp fibrose-carnose, hard when dry, about 2–2.5 mm. thick; endocarp woody, slightly 10-sulcate and bullate, with resinous cavities.

Sacoglottis gabonensis is the only species of Humiriaceae found outside America. It is a frequent timber tree in the tropical West African rain forests (mostly flooded forests), throughout the Gulf of Guinea, from Sierra Leone to northern Angola. The tree is one of the tallest of the forests, and its timber is hard and mostly used locally for construction. The subglobose-ellipsoid fruits have edible exocarps and seeds; the endocarps often are found floating in the river and on the sea shores. Aubry le Compte gave the native name of "djouga" or "douga" of Gabon. Exell quoted "n'ooca" as a native name at Sumba, and Exell and Mendoça quoted "n'coca" as used in Angola. According to Emilio Guinea, the name from Spanish Guinea is "esua."

AFRICA: LIBERIA: Johnsonville, *Dinklage* 2973 (A). Vicinity of Firestone Plantations, along Dukwai River, tree 100 ft. × 4 in. much fluted and buttressed, "daush" (cherry), *Cooper* 68 (A, BM, GH, NY, US, Y); tree 50 ft. × 12 in. to 100 ft. straight bole, great buttressed, "daush" (cherry), 1929, *Cooper* 274 (A, BM, GH, NY, US, Y). Monrovia on clayish ground near the Mesurado River, medium-size tree, flowers green, the anthers only ochre coloured, *Dinklage* 2973 (A).

IVORY COAST: Abidjan, "aguapo," 7-V-1929, *Aubreville* 92 (A). Tropical West Africa, *Mann* 925, 1417 (GH).

SIERRA LEONE: Kambui, forest reserve; big timber tree, bearing fruits, bark peeled and put in Raphia wine, "kpou-wuli," 29-X-1937, *Edwarson* 181 (BM). Without locality, *Afzelius* s.n. (BM).

GOLD COAST: Without locality, *Vigne* 2801 (NY). Western Province Ankasa, Fuale; tree in wet forest, crown spreading; fruit reported edible; alt. 100 m., "nzima," I-1942, *Adjimang* 4849 (A). Without locality, *Oigne* 2800 (BM).

NIGERIA: Oban, *Talbot* 1744 (BM).

CAMEROONS: Bipinde, Urwaldgebiet, *Zenker* 148 (US); 440 (M); 1249 (A, BM, M, S); 1624 (BM, M, NY, S); 1671 (NY); 1677 (BM, M, S); 1953 (BM); 2499 (BM, M, S); 2760a (BM); 4407 (BM, S).

FRENCH EQUATORIAL AFRICA: Gabon, 180 km. to the southeast of Port Gentili; concession of Mr. Marchier on Lake Anengue, between Rivers

Kouroue and Edjiwe; large tree, bole crooked, local lumbermen say this tree rotten when old, "ozouya" (N'komi), 21-VI-1930, *Krukoff* 121 (NY, A, US). Brazaville, forêt de Mayombe-Holle, 26-II-1954, Herbar I.E.C. No. 4769, *Koechlin* 2632 (U).

ANGOLA: Congo Portugues, Sumba, Peco, proximum flumen, Zaire, alt. 0.0 m., 1923, *Gossweiler* 751 (US); *Gossweiler* 8707 (BM). Sumba, lower Congo River, an erect green tree, "n'ooca," 15-V-1923, *Gossweiler* 8751 (BM). At Belize-Maiombe-Congo Post, a tree 40 m. high with usually somewhat obliquely ascending trunk, primary branches few and horizontally spreading, flowers greenish, fruits globular the size of a walnut, highest forest trees at Belize, *Gossweiler* 6996 (BM). Belize, on the Luali River, tree evergreen, 25-35 m., timber of a dusky mahogany color, leaves rigid, fruits the size of a walnut, flowers collected 2 years ago from the same tree, common near the official residence, "niuca," 13-II-1918, *Gossweiler* 8182 (BM).

6. *Sacoglottis guianensis* Benth. in Hook Journ. Bot. Kew Misc. 5:103. 1853.—Urb. in Mart. Fl. Bras. 12(2):448 (in part), tab. 94, fig. 1, habitat. 1877.—Walp. Ann. Bot. Syst. 4:385. 1857.

Sacoglottis amazonica Benth. in Hook. Journ. Bot. Kew Misc. 5:104. 1853.

Sacoglottis guianensis fma. *dolichocarpa* Ducke, Arch. Jard. Bot. Rio Janeiro 3:179. 1922; 5:143, pl. 14, fig. 38. 1930.—Arch. Inst. Biol. Veget. Rio Janeiro 4:27. 1937.

Sacoglottis guianensis var. *maior* Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 4:27. 1938.

Type: *Rob. Schomburgk* 574; paratype: *Rich. Schomburgk* 842, British Guiana.

Large or medium-size tree with minutely hirtellous-puberulous or glabrous terminal branches. Leaves coriaceous, firm. Petiole 4-12 mm. long, minutely puberulous or glabrous, sulcate above. Blade elliptic, ovate-elliptic, subovate or oblong-ovate, rounded, obtuse or cuneate at base, narrowed, acuminate or cuspidate at apex, slightly serrate-crenate or subentire at margin; 5-15 cm. long, 3-6 cm. broad; above nitid, glabrous with flat midrib, lateral nerves and veins little or not conspicuous; beneath scattered, appressed, minute hairs or more frequently glabrous, midrib thick, eminent, secondary nerves 10-12 pairs, little ascendent more or less prominulous, near the margin arcuate-anastomosate, minor nerves finely reticulate slightly prominulous.

Inflorescences axillary, cymose-paniculate, shorter than flowers, dichotomous, peduncle and branchlets shortly hirtellous-pubescent. Bracts amplexant, ovate-triangular, ciliate, 0.5-1 mm. long, persistent. Pedicels very short, (0.1-0.2 mm. long), glabrous, articulate with 1-3 mm. long peduncles or sessile on pilose or glabrate terminal branchlets. Sepals ovate-rotundate 6-7 mm. long, puberulous and minutely ciliate. Petals greenish, rather thick, linear or oblong-lanceolate, subacute, glabrous or puberulous, 3-4.5 mm. long, 1.5 mm. broad at base. Stamens 10, filaments complanate, thickened, about lower half connate, 2.5 and 3 mm. long, alternating. Anthers ovate-

lanceolate, 1 mm. long, thecae elliptic about 0.4 mm. long, connective thick, trigonous-lanceolate. Disk annular, membranous, denticulate, 0.5–0.6 mm. high. Ovary globose, glabrous, 5-locular, cells uniovulate. Style 2–3 mm. long, erect, glabrous. Stigma subcapitate, 5-lobate. Drupe ellipsoid-oblong, attenuate at base, subacute or subobtuse at apex, 15–30 mm. long, 9–12 mm. in diameter (most typical 30×10 mm.); exocarp smooth compact, resinous, 1–1.5 mm. thick; endocarp woody, smooth or very slightly bullate and furrowed, narrow-oblong, acute at both ends, resinous-lacunose, usually 1-seeded, rarely with 2 or 3 seeds.

S. guianensis is a widespread polymorphous species throughout tropical South America, and includes varieties difficult to distinguish and often mistaken for closely related species. The lack of complete material for every collection or tree and the fact that the existing herbarium specimens only bear flowers or fruit make it difficult to establish correlations between flowering and fruiting characters and the constancy of them. Through his extensive knowledge of the Amazonian flora, Ducke was the first to point out the existence of several varieties and forms among the supposed *S. guianensis* populations. Study of abundant material with special attention given to the fruit as a taxonomic character has made it possible to consider two new species segregated from the former broader concept of *S. guianensis*. A few varieties remain in this species with somewhat artificial characters due to the lack of fruiting material. For the same reason the typification of the species cannot be free from error because the Schomburgk collections are flowering specimens lacking fruit, which in fact are key characters. *Schomburgk* 842, 571, and 574, coincide so much that they seem to belong to one and the same collection; they agree completely with fruiting collections (as for example the *Melinon* from French Guiana) having elongated fruit; I therefore do not hesitate to consider the oblong fruit the characteristic trait of *S. guianensis*. The typical form of this species has pubescent-hirtellous branches and glabrous petals, but the pubescence of the branchlets is lacking in some varieties, and the petals become more or less puberulous in others. The length and thickness of the fruit show some variation, but the elongate, acutish or subobtuse drupe is the main character of the species and distinguishes it from the newly segregated *S. cydonioides* and *S. mattogrossensis*. From the latter one it is furthermore distinguished by its more rigid and thicker, not conspicuously reticulate leaves.

The variety *guianensis* in all its forms, typical or glabrous, is spread throughout the Amazon Basin on elevated (uninundatable) places in rain forests or in the savanna and campo thickets varying from large to small-size trees. It is found abundantly in the Amazon

Basin in the States of Amazonas and Pará and spreads through Rio Branco to the Guianas and Venezuela and to the Apaporis region in Colombia. In the Guianas it is found on the slopes of the mountains up to 1,000 m. elevation. Variety *maior* is almost restricted to the Manaos region, and variety *hispidula* is more extended in the Amazonian States of Venezuela and Brazil, it being less frequent in Surinam and Pará.

Key to the Varieties and Forms of *Sacoglottis guianensis*

1. Petals glabrous 6a. var. *guianensis*
2. Terminal branchlets hirtulous pubescent 6a(1). fma. *guianensis*
2. Terminal branchlets glabrous 6a(2). fma. *glabra*
1. Petals hispid-puberulous.
3. Terminal branchlets glabrous. Petioles 6–12 mm. long . 6b. var. *maior*
3. Terminal branchlets hirtulous-pubescent.
Petioles 4–8 mm. long 6c. var. *hispidula*

6a(1). *Sacoglottis guianensis* var. *guianensis* fma. *guianensis*

FIGURE 37, *a-m*; 38, *b-d*; PLATE 21

Sacoglottis guianensis fma. *dolichocarpa* Ducke, Arch. Jard. Bot. Rio. Janeiro 3:179. 1922.

VENEZUELA: AMAZONAS: Cerro Moriche, Río Ventuari, tree to 10 m., fruit green, frequent on lower slopes, alt. 200 m., 16-I-1957, *Maguire, Cowan, & Wurdack* 30967 (NY, US); tree 3 m., fruit green, frequent on dry open east slopes, alt. 300–1,000 m., 13-I-1951, *Maguire, Cowan, Wurdack* 30844 (US). Savanna at Santa Bárbara, Río Orinoco at mouth of Río Ventuari, alt. 125 m., tree 5 m. mature, fruit orange, 21-II-1951, *Cowan & Wurdack* 32022 (US). BOLÍVAR: Río Apacará, Municipio Woisaan, vegetación riparia, alt. 500 m., “Peru-yek,” 28-VIII-1954, *Bernardi* 1571 (NY). Región de los ríos Icaburú, Hacha y cordillera sin nombre a 280° de las cabeceras del río Hacha rumbo al sur, 450–850 m. alt.; selva pluvial o sabana natural, 7-I-1956, *Bernardi* 2813 (VEN, NY).

BRITISH GUIANA: “Guiana anglica,” X-1842, *Schomburgk* 842, (US, M, paratype); photo F.M. 12599 in Berlin; Roraima, 1842–43, *Schomburgk* 571, (P, paratype); 574 (P, isotype).

SURINAM: Boschreserve, Sectie O, 1-XI-1915, *Boschwezen* 1166 (U); Boomnummer 593, 21-V-1920, *Boschwezen* 4673 (U); 4-XI-1921, *Boschwezen* 5430 (U); 16-VIII-1918, *Boschwezen* 3961 (U); 1-VIII-1917, *Boschwezen* 3079 (US, U); 24-VIII-1917, *Boschwezen* 3125 (U, IAN). Suriname-rivier, 24-X-1947, *Boschwezen* 117 (U). Boschreserve Zanderij I, Boomnummer 56, 27-VI-1919, *Boschwezen* 4469 (U); 9-VII-1917, *Boschwezen* 2974 (US, U, IAN); IX-1942, “doekoelia,” “japopalli,” “gannasagon,” *Stahel* 18 (IAN, U, NY, A). In monitibus qui dicuntur Nassau; in bos bij K 11.2, Boom 30 m, 30 cm. dik, 22-III-1949, *Lanjouw & Lindeman* 2869 (U). Tafelberg (Table Mountain), frequent, tree 20 m., 30 cm. diameter, flowers greenish fragrant, high mixed walaba forest, base talus, 24-IX-1944, *Maguire* 24844 (M, NY).

FRENCH GUIANA: “Herbier de la Guyane, Année 1863,” *Melinon* s.n. (P). “Herbier de la Guyane Française, Année 1862, No. 11, bois rouge tisane,” *Melinon* 584 (P). “Guiane française,” *Le Prieur* 253 (P).

BRAZIL: PARÁ: Obidos, Serra da Boa Vista, 24-XII-1913, “achuá,” *Ducke* 15234 (MG). Santarém, cerrado, arbusto grande, 16-XI-1909, *Huber* 10446

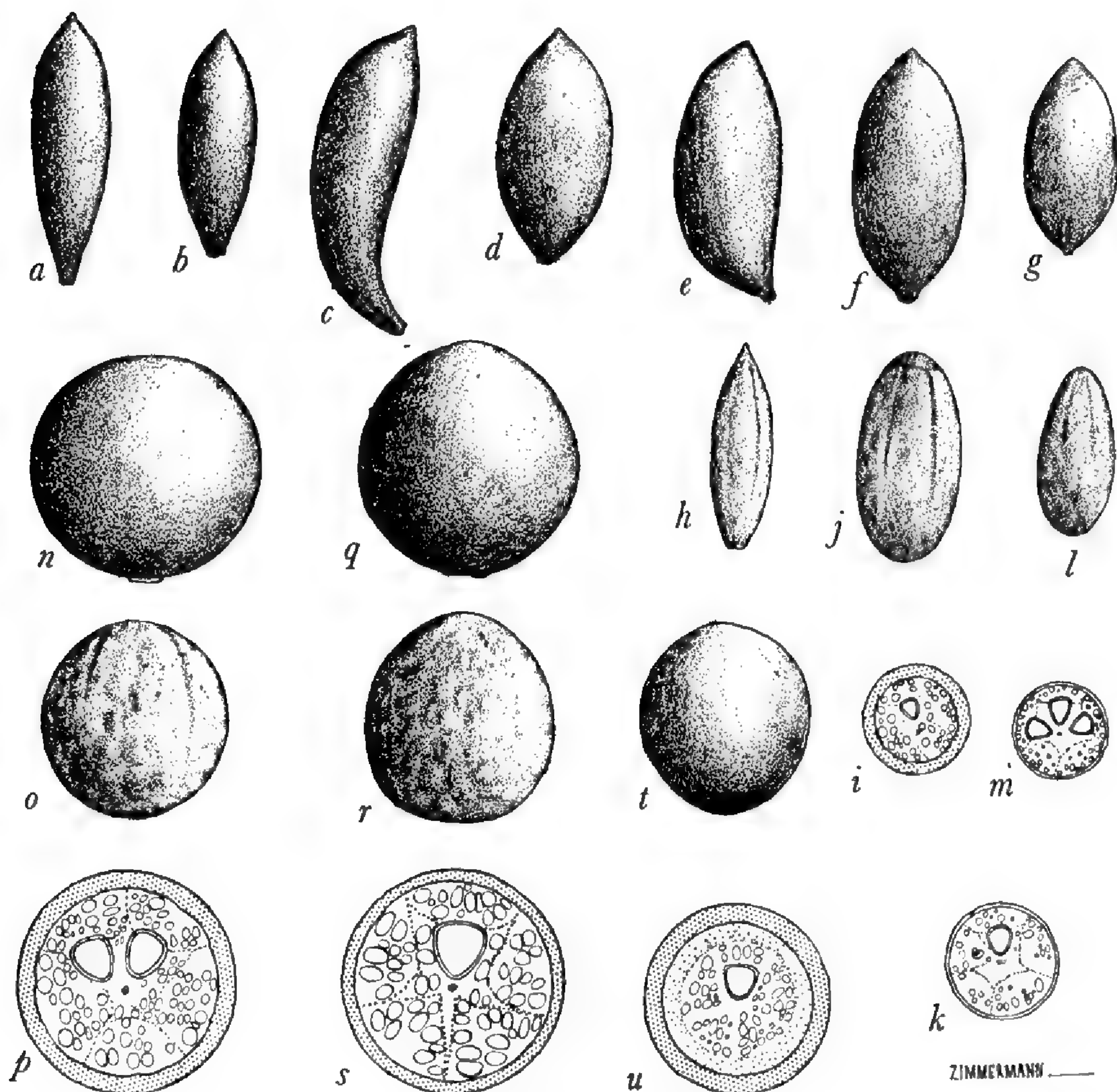


FIGURE 37.—a-m, *Sacoglottis guianensis* var. *guianensis*, $\times 1$, a-g, fruit: a, Ducke 9868; b, Pires 41; c, Melinon s.n.; d, Black 50-8831; e, Boschwezen 1166; f, Bernardi 1571; g, Cowan & Wurdack 32022. h-m, Endocarps: h, Boschwezen 1166; i, transection; j, Bernardi 1571; k, transection; l, Cowan & Wurdack 32022; m, transection. n-p, *Sacoglottis mattogrossensis*: n, Fruit (Piers 4017); o, endocarp; p, transection. q-s, *Sacoglottis mattogrossensis* fma. *subintegra*: q, Fruit (Ducke 23820); r, endocarp; s, transection. t-u, *Sacoglottis cydonioides*: t, Fruit (Boschwezen 6495); u, transection.

(BMMG). Municipio de Monte Alegre, Rio Maicurú, caminho de Cáaussu a localidade Balança, terra firme, arvore 5 m., 16-IX-1953, Fróes 30284 (US). Rio Tapajoz pres des cataractes du Mangabal, 31-VIII-1916, Ducke 16419 (MG, P, US). Municipio de Faro, Fazenda Santa Olimpia, Campo Umiri, arvore, pequena, fruto verde, 6-XI-1950, Black & Ledoux 50-10553 (US). Lago de Faro, matta da beira, 16-VIII-1907, Ducke 8368 (MG). Campos a E. de Faro, 27-VIII-1907, Ducke 8524 (BM, MG). Campina rana, Alto Ariramba, 21-XII-1906, Ducke 8042 (BM, MG). AMAZONAS: Basin of Rio Madeira, Municipality Humayta on plateau between Rio Livramento and Rio Ipixuna, tree 60 ft. high on campinarana alta, 7-18-XI-1934, Krukoff 7082 (U, BM, IAN, A, US, S, NY). Maués, varzea, arvore pequena, 30-XI-1946, Pires 41 (IAN). Rio Negro, Preto, Matupiry, tree 35 ft. 6 in., border of river, restinga alta, 14-XI-1947, Fróes 22857 (US). Rio BRANCO: Caracarahy, road Boa Vista, tree 4 m., whitish flowers, low hard growth on highland, 3-III-1948, Fróes 22940 (IAN). Caminho de Samauma a

campo de aviação de Mucajai, kms. 14-15 da estrada Boa Vista-Caracarai, arbusto a beira da capoeira, 25-VIII-1951, *Black & Magalhães* 51-12972 (IAN). Boa Vista-Caracarahy, perto da Colonia Fernando Costa, arvore baixinha, fruto verde, 11-IX-1951, *Black* 51-13454 (US, IAN). Goiás: Porto Nacional, arvore da matta, flores amareladas aromaticas, 27-VII-1955, *Macedo* 3922 (IAN, S, US). Without locality, *Riedel* s.n. (K).

6a(2). *Sacoglottis guianensis* var. *guianensis* fma. *glabra* Cuatr., forma nov.

FIGURE 38,a

A forma guianensi typica differt ramulis terminalibus glabris.

Type in the Herbarium of the Instituto Agronomico do Norte, Belém do Pará, Brazil, collected in the Ilha Collares, State of Pará, Brazil, December 29, 1953, by Ricardo Lemos Fróes (No. 30670).

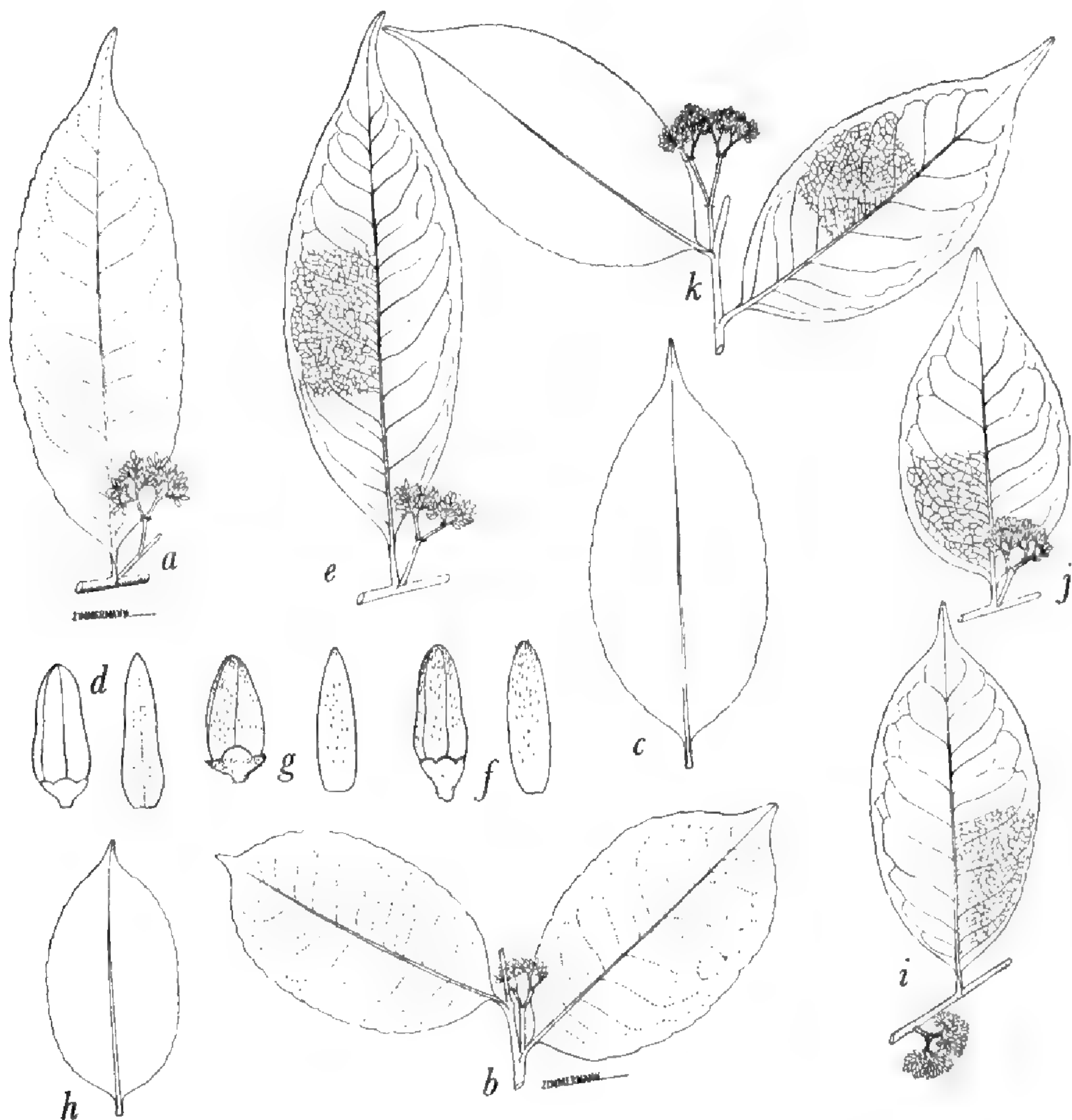


FIGURE 38.—a, *Sacoglottis guianensis* fma. *glabra*, $\times \frac{1}{3}$ (*Ducke* 14872); b, *S. guianensis* fma. *guianensis*, $\times \frac{1}{3}$ (*Schomburgk* 842); c, *S. guianensis* fma. *guianensis*, leaf, $\times \frac{1}{3}$ (*Bernardi* 1571); d, *S. guianensis* fma. *guianensis*, bud and petal, $\times 1\frac{2}{3}$ (*Ducke* 8524); e, *S. guianensis* var. *maior*, $\times \frac{1}{3}$ (*Ducke* 23818); f, *S. guianensis* var. *maior*, bud and petal, $\times 1\frac{2}{3}$ (*Ducke* 23818); g, *S. guianensis* var. *hispidula*, bud and petal, $\times \frac{2}{3}$ (*Maguire* 29337); h, *S. guianensis* var. *hispidula*, leaf, $\times \frac{1}{3}$ (*Maguire* 29337); i, *S. mattogrossensis* fma. *mattogrossensis*, $\times \frac{1}{3}$ (*Ducke* 2188); j, *S. mattogrossensis* fma. *subintegra*, $\times \frac{1}{3}$ (*Ducke* 23820); k, *S. cydonioides*, $\times \frac{1}{3}$.

COLOMBIA: AMAZONAS-VAUPÉS: Río Apaporis, Jirijirimo, 250 m., alt., árbol 15 m., flores verde-amarillentas, 25-26-XI-1951, *García Barriga* 13681 (US).

SURINAM: Boschreserve Zanderij I, Boomnummer 56, 8-XII-1951, *Boschwezen* 1490 (U).

FRENCH GUIANA: "Herbier de la Guyane, année 1863," *Melinon* s.n. (US, P). Route de Cayenne au km. 7700 côte gauche de la route, en face de la Pepinière, "bofo-oudon" (Paramaka) "mahot-cochon," "bois cochon" (nomme commercial), 4-XII-1956, *BAFOG* 7622 (U).

BRAZIL: PARÁ: Santarém, VIII-1950, *Spruce* 5963 (MG). Santarém, VIII-1950, *Spruce* s.n. (MG, BM, S); *Spruce* 763 (M); *Spruce* 1009 (P). "Frequent on margin of moist forests, Santarem; I also saw much of it at Obidos, an./50; spreading tree of 30 ft., young leaves deep red, petals whitish-green, anthers yellow, fruits said to be very good eating 'uaxua,'" *Spruce* 1009 (Herb. Benthamianum, K). Region des Campos de l'Ariramba (Trombetas), 30-IX-1913, "ichuá," *Ducke* 14872 (BM MG, P, US). Matta entre Cuminámirim e Ariramba, 12-X-1913, *Ducke* 14967 (MG). Monte Alegre, Campo, 11-XII-1908, *Ducke* 9868 (MG). Remansao, Rio Tocantins, tree 14 m., on high land, high forest, west side, 15-IX-1948, *Fróes* 23494 (US). Rio Pori, afluyente del Xingú, região de levantamento estatístico florestal feito pelo IAN, SPVEA e FAO, arvore 10 m. ao lado de capinarana, 30-XI-1955, *Fróes* 32478 (US). Cambinho de Jubim para Condeixa, Iiha do Marajó, arvore 12 m., fruto verde, 14-XI-1948, *Black* 48-3555 (IAN). Vigia, moita de mato em cima de un pequeno monte arvore 10 m., fruto verde, 24-I-1950, *Black* 50-8831 (IAN). Collares, matta, umirizal, "achuá," 15-VIII-1913, *Ducke* 12656 (MG). Ilha de Collares, terra firme capoeira, terreno argiloso, municipio de Vigia, arvore 4 m., 29-XII-1953, *Fróes* 30670 (IAN holotype). Vigia, Campina do Palha, ilha de mata; arvore pequena, "uchira," 21-I-50, *Black* 50-8685 (IAN). Jaramacani, corola branca, 27-V-57, *Egler* 281 (MG, US). AMAZONAS: Basin Rio Solimões, Municipality São Paulo de Olivença, basin of creek Belém, tree 100 ft., trunk 2 ft. diameter, terra firma, high forest, 26-X-11-XII-1936, *Krukoff* 8757 (U, NY, US, S, P, BM).

6b. *Sacoglottis guianensis* var. *maior* Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 4:27. 1938.

FIGURE 38,e-f

Type: *Ducke* 23818, Brazil, Manaus.

Petala hispidula-puberula. Ramuli glabri. Petiolus 6-12 mm. longus. Reticulum venosum supra paulo conspicuum. Fructus verisimiliter oblongus.

Ducke distributed under the type collection (23818) flowering branches and loose fruits, which he described. I have seen one single sample of this fruit (at US), and it is ellipsoid, rounded at the base, pointed at the top, 3.5 cm. long, 2.1 cm. broad; the exocarp is about 2 mm. thick and the endocarp is hard, woody, with resinous cavities. This fruit was not collected at the same date as the flowering specimens, and I hesitate to admit that they belong together; if they did, this collection would be a new species. I suspect that the fruit here referred to belongs to *S. macrophylla*, a species much spread in the same region (Manaos) where the Ducke specimens were collected.

BRAZIL: AMAZONAS: Manaus, silva non inundabili, arbor sat elata floribus viridibus, 2-X-1932, *Ducke* 23818 (holotype, RB; isotypes, U, S, US); loco arenoso

ad Cachoeira do Mindú, arbor sat magna flor. viridibus, 25-IX-1929, *Ducke* 23433 (US, S). Manaos, silva terris altis ultra Flores, arbor sat magna floribus viridibus, 14-IX-1945, *Ducke* 1756 (MG, NY, IAN, A, US). Breves, in estuario amazonico circa Pará; silva non inundata, arbor magna, floribus viridibus, fructibus globosis, *Ducke* 17784 (U). Cajatuba, habitat low and high land, "achuá," 18-I-1932, *Montes da Costa* 281 (IAN, P). MARANHÃO: Grajahú, Rio Mearim, 180 m. alt., arvore alta, flor amarella, *Arojado Lisboa* 2330 (BM, MG). PARÁ: Peixeboi (Belém-Bragança), "Pararú," 16-VII-1907, *Siqueira* 8281 (BM, MG, US).

6c. *Sacoglottis guianensis* var. *hispidula* Cuatr., var. nov. FIGURE 38, g-h

Petala extus plus minusve hispidulo-puberula. Ramusculi terminales pubescenti-hirtuli. Petioli 4-8 mm. longi. Fructus ignotus verisimiliter oblongus.

Type in the U.S. National Herbarium, No. 1660793, collected near Livramento on Rio Livramento, firm land, Municipality of Humayta, at Rio Madera Basin, State of Amazonas, Brazil, November 1934, by B. Krukoff (No. 6653). Isotypes in NY, A, IAN, BM, S, U.

The collections included in this variety show much polymorphism in the leaf-shape within the broad range of variation of *S. guianensis*. The Surinam collection, *Maguire* 24836, is a form with scanty hairs on the petals and more rigid and more venose leaves. On the other hand, *Maguire* 29337 from the Orinoco is another extreme form with more hispidulous petals and small, rigid, almost enervate leaves. *Maguire, Cowan, & Wurdack* 30844 and 30967 and *Froes* 22587 are named as forma *guianensis*, but they have very few hairs on the petals; they range in the very intermediate forms.

VENEZUELA: AMAZONAS: Río Orinoco, Culebra savanna, north base of Cerro Duida, alt. 200 m., medium-size tree, flowers white, occasional at the edges of savanna, 13-X-1950, *Maguire, Cowan, & Wurdack* 29416 (VEN). Río Orinoco Río Atabapo, Caño Temi, 1 hour below Yavita, alt. 125 m., edge of small laja, medium-size tree with greenish flowers, 20-X-1950, *Maguire* 29337 (US). BOLÍVAR: occasional along river 1-4 km. above Salto de Humito (25-30 km. from mouth), tree 9 m., flowers green with yellow anthers, 7-I-1956, *Wurdack & Monachino* 41149 (US). Along Río Karuai at base of Sororopán-tepuí, west of La Laja; alt. 1,220 m.; tree 4 ft. tall; leaves subcoriaceous, rich green and very shining above, pale green below; "perú-yek," 29-XI-1944, *Steyermark* 60756 (NY, VEN).

SURINAM: Coppenam River headwaters, Wallaba forest, km. 9, line between Camps No. 5 and 4, frequent; tree 15 m., 20 cm.; flowers greenish, fragrant, 23-IX-1944, *Maguire* 24836 (GH, NY, US, U, VEN).

BRAZIL: AMAZONAS, Río Urubú, Cachoeira Iracena, terra firme, alta; floresta central; arvore 18 m., flores brancas, 22-IX-1949, *Fróes* 25369 (US). Campinha Rio Breves, IX-1913, *Kuhlmann* 3510; tree 40 ft., green-whitish flowers, border of river of whitish water, on low land, high forest, 11-X-1947, *Fróes* 22587 (IAN). Basin Río Madeira, Humayta near Livramento, *Krukoff* 6653 (type).

7. *Sacoglottis mattogrossensis* Malme, Arkiv. Bot. Stockh. 22A, No 7:9. 1928. FIGURES 37,n-p

Sacoglottis guianensis forma. *sphaerocarpa* Ducke, Arch. Jard. Bot. Rio Janeiro 3:178. 1922; 5: pl. 14 figs. 39a-b. 1930.

Type: *Malme* II:2237, Brazil, Mato Grosso, Santa Ana da Chapada.

Small or medium-size tree with lenticellate and hirtellous or glabrous branchlets. Leaves coriaceous, flexible, glabrous or subglabrous. Petiole 5–8 mm. long, semiterete, puberulous or glabrate, thickened at base. Blade oblong-elliptic or elliptic-lanceolate, ovate-elliptic, rounded, obtuse or cuneate at base, acutely acuminate or cuspidate at apex, obtusely serrate at margin or subentire; 5–11 cm. long, 2–2.5 cm. broad, glabrous or with sparse hairs on midrib beneath; midrib prominulous above, prominent beneath, secondary nerves 8–10 on each side, subascendent, thin and prominent, minor nerves and veins forming subclax reticulum prominently conspicuous on both sides. Sometimes, chiefly on young branches, blades biglandular at base.

Inflorescences axillary, small, cymose-paniculate, dichotomous, peduncle 2–5 cm. long, stout, striate, hirtellous, the branchlets short, hispidulous. Bracts persistent, amplexant, ovate-triangular, acutish, minutely puberulous, ciliate, 1–0.6 mm. long. Pedicels thick, 0.7 mm. long, glabrous. Sepals ovate, rounded at apex, thick, about 0.6 mm. long, glabrous except for ciliate margin. Petals linear, narrowed toward apex, subacute, glabrous, about 4 mm. long, 1–1.2 mm. broad at base, the estivation cochlear. Stamens 10, glabrous, filaments complanate, 2.5 and 3.2 mm. long alternating, lower part united in tube. Anthers ovate, 0.7–0.9 mm. long, thecae oblong, connective thick, acute or subacute. Disk about 0.4 mm. high, annular, rather thick, dentate. Ovary ovoid, glabrous, 0.8 mm. high. Style 2–3 mm. long. Stigma short-capitate, 5-lobate. Drupe globose, 17–28 mm. diameter, exocarp compact, resinous, 1–2 mm. thick, coriaceous and granulose when dry; endocarp woody, almost smooth, slightly bullate and sulcate, innerly resinous-lacunose, usually monospermous or with 2 (rarely 3) seeds.

This species has been confused with *S. guianensis*, from which Ducke first separated it as a variety based on its globose fruit form. It furthermore differs from *S. guianensis* in its thinner, flexible, and prominently nerved leaves; for this reason I promoted forma *sphaerocarpa* Ducke to the rank of a species (type: *Kuhlman* 2128). After examining the type of *S. mattogrossensis* Malme (flowering material), I realized that the Kuhlmann and Malme plants are conspecific.

S. mattogrossensis is rather a species of the lower Amazon Basin,

extending from Maranhão southward to Rio de Janeiro; variety *subintegra* goes further west to the Manaus region and is found in Colombia at the northern end of the rain forest domain.

The species is rather polymorphic, and the following key outlines the most conspicuous varieties and forms.

Key to the Varieties and Forms of *Sacoglottis mattogrossensis*

- 1. Petals glabrous 7a. var. *mattogrossensis*
- 2. Branchlets hirtulo-puberulous 7a(1). fma. *mattogrossensis*
- 2. Branchlets glabrous 7a(2). fma. *glabra*
- 1. Petals puberulous 7b. var. *subintegra*
- 3. Branchlets glabrous 7b(1). fma. *subintegra*
- 3. Branchlets hirtulo-puberulous 7b(2). fma. *puberula*

7a(1). *Sacoglottis mattogrossensis* var. *mattogrossensis* fma. *mattogrossensis*
FIGURE 38,i; PLATE 22

BRAZIL: PARÁ: Santarém, ilha de matta no campo, "achuá," 17-VII-1916, *Ducke* 16346 (MG). Obidos, matta, 8-III-1909, arvore pequena, *Ducke* 10218 (MG); matta de terra firme, 23-IX-1910, *Ducke* 11050 (MG); in terreno arenoso, "achuá," 10-VIII-1916, *Ducke* 16320 (US, BM, MG). Rio Xingú, em frente Seuzel, mun. Porto de Méz; região onde foi feito um levantamento estatístico florestal pelo IAN, SPVEA e FAO; arvore de 20 m. alt., terra firme, flanco do planalto, margem esquerda do rio, 18-XI-1955, *Fróes* 32391 (IAN). Monte Alegre, arbor parva 26-III-1928, *Kuhlmann* 2128 (US, S, U, isotypes of fma. *sphaerocarpa* *Ducke*). Soure, Capoeira densa, arvore pequena, fruto verde, polpa (verde) muito adstringente, amarela, 26-II-1950, *Black* 50-9058 (US). Serra do Cachimbo, 425 m., 12-XII-1956, *Pires, Black, Wurdack, & Nilo* 6140 (IAN). Alto Tapajós, Vila Nova, perto da Cachoeira do Chacorão, terra firme, campo; arvore pequena, frutos esfericos amarelos, 24-I-1952, *Pires* 4017 (IAN, US). MARANHÃO: São Luiz, Granja Barreto, arvore pequena, 26-VI-1949, *Murça Pires* 1510 (IAN, NY); high land, tree 4 m. yellow fruit, 14-V-1949, *Fróes* 24297 (IAN). São Luiz, Granja Federal, tree 4 m., white flowers, 12-V-1949, *Fróes* 24256 (IAN). Granja Barreto, viveiros de aves, arvore pequena, flor verde, registro n. 32, "parurú," 29-X-1948, *Ducke* 2188 (IAN). Anil, Capoeira, "uachua," 12-IX-1903, *Ducke* 363 (US, BM, MG). RIO BRANCO: Rio Canta, arbusto ou arbore, "achua," 8-X-1951, *Black* 51-13843 (US). MATTO GROSSO: Santa Anna da Chapada, arbor parva habitu *C. salicifolia*, in capueira, 10-VIII-1902, *Malme* 2237 (S, holotype; S, isotype, sterile). RIO DE JANEIRO: Rio de Janeiro ad urbem loco Gavea, VIII-1916, *Frazão* 8118 (US), in silvulis siccioribus prope Porto Estrella, arbor parva fructibus aurantiacis, 28-VIII-1925, *Ducke & Kuhlmann* 19165 (US).

7a(2). *Sacoglottis mattogrossensis* var. *mattogrossensis* fma. *glabra* Cuatr., fma. nov.

Ramuli terminales glabri.

Type in the U.S. National Herbarium, No. 1040536, collected near Faro, State of Pará, Brazil, May 11, 1911, by Adolfo Ducke (No. 11653). Isotypes at BM and MG.

COLOMBIA: VAUPÉS: Riberas del Río Inírida alrededores de Morichal, cerca de la boca del río Papanaua, 200 m. alt., árbol 15 m., frutos color verde, 9-II-1953, *Fernández* 2228 (COL, US).

BRAZIL: PARÁ: Soure, ilha do Marajo, Capoeira do campo con caembê; arvore pequena, fruto verde, inflorescencias velhas, 12-X-1948, *Black* 48-3453 (IAN); entre os km. 1 e 7 extremo Monte Alegre a CANP; campos cerrados ("cobertos"), 5-V-1953, *Lima* 53-1332 (IAN). Belém on lands of IAN, 3 km. east of Administration Building, near Fazenda Velha, medium-size tree, flowers green, fruits red, 21-I-1944, *Antonio Silva* 59 (IAN, US). Faro, "achuá," 11-V-1911, *Ducke* 11653 (type US, BM, MG), photo F.M. 35178 from Paris. Portel, matta da terra firme, arvore de porte mediano, casca castanha, 17-X-1955, *Williams & Silva* 18201 (US). Serra de Arumandube, Almeirim, matta da Chapade "achuá" 26-VIII-1918, *Ducke* 17262. Sitio Caçote, Areias-Recife-Pe, 6-X-1949, arvore pequena, flores brancacentas, 6-X-1949, *Lima* 49-336 (IAN). Monte Alegre, campo, arvore grande, "achuá," 11-XII-1908, *Ducke* 9866 (MG). Belém, Hosp. Dom. Fr., II-05, *Huber* 6992 (MG). EFB, Santa Izabel, Carapará, Capoeira, arbusto, flor amarela, 27-XII-1908, *Museu Goeldi* 10130 (BM, MG). PERNAMBUCO: Prazeres, 13-X-1932, *Pickel* 591 (GH, NY, US). Ilha Itamaraca, XII-1857, *Gardner* 1146 (BM). Iguarassu, 1-X-1887, *Ramage* s.n. (BM). MARANHÃO: Anil, Capoeira, 3-VI-1907, *Ducke* 519 (MG). SÃO PAULO: Santos, in ripa arenosa sicca aprica maris, 18-X-1875, *Mosen* 3477 (S).

7b. *Sacoglottis mattogrossensis* var. *subintegra* (Ducke) Cuatr., comb. nov.
Sacoglottis guianensis var. *subintegra* Ducke, Arch. Inst. Biol. Veget. Rio Janeiro 4:27. 1938.

7b(1). *Sacoglottis mattogrossensis* var. *subintegra* fma. *subintegra*
FIGURES 36,*h-n*; 37,*q-s*; 38,*j*

Petla puberula. Ramuli terminales glabri. Fructus globosus 18-28 mm. diamitens sublaevis, exocarpio coriaceo-resinoso 1-2 mm. crasso, endocarpio leviter undulato, 1.7-2.4 cm. diamitenti, lacunoso-resinoso monospermo.

Type: *Ducke* 23820, Brazil, Amazonas, Manaus.

BRAZIL: AMAZONAS: Manaus, silva terris altis ultra coloniam João Alfredo, arbor magna floribus viridibus odoratis fructus rubro-aurantiacis, "achuá," 2-VIII-1937, *Ducke* 23820 (RB, holotype; U, P, S, US, isotypes); silva primaria terris altis argillosis, arbor magna viridibus, 23-VII-1943, "ex arbore typica" flowers, *Ducke* 1295 (A, NY, IAN, US, MG). Monte Alegre, região da Colonia da Mulata, terra firme, matta virgen, arvore, flor branca, 28-IX-1955, *Fróes* 30416 (US).

7b(2). *Sacoglottis mattogrossensis* var. *subintegra* fma. *puberula* Cuatr., fma. nov. PLATE 23

Ramuli terminales hirto-puberuli.

Type in the Herbarium of Museu Goeldi at Belém do Pará, Brazil, collected at Canutá, beira da Campina, State of Pará, Brazil, July 21, 1916, by Adolpho Ducke (No. 16286). Isotype in the Herbarium of British Museum.

BRAZIL: PARA: Canuta, *Ducke* 16286 (MG, holotype; BM, isotype).

8. *Sacoglottis cydonioides* Cuatr., sp. nov. FIGURE 38,*k*; PLATE 24

Arbor media vel grandis ramis terminalibus brunneis subteretibus plus minusve lenticellatis glabris.

Folia crasse vel crassiuscule coriacea rigida glabra. Lamina ovato-elliptica, ovato-oblonga, oblongo-elliptica vel subovato-lanceolata apice subite acuminata vel cuspidata, basi rotundata vel obtusa et abrupte in petiolum robustum subalatum basi incrassatum 3–6 mm. longum cuneato-angustata, margine plus minusve revoluta obtuse serrata vel subintegra; 6–13 cm. longa 2.5–6 cm. lata; supra nitida saepe laevis costa crassiuscule prominula nervis secundariis reticuloque immersis obsoletis vel plus minusve conspicuis; subtus costa valde eminenti nervis secundariis 10–12 utroque latere tenuibus prominulisque patulis marginem versus arcuato-anastomosantibus venulis minute reticulatis bene prominulis vel subimmersis sed conspicuis.

Inflorescentiae axillares et terminales cymoso-paniculatae dichotomoramosae foliis valde breviores pedunculo 0.5–1.5 cm. longo robusto striato plus minusve complanato puberulo, ramis brevibus angulatis minute hispidulo-puberulis. Bracteae persistentes amplexantes ovatae acutiusculae parce ciliatae 1.3–0.5 mm. longae. Pedicelli crassi 0.4–0.5 mm. longi glabri. Sepala ovata obtusa crassiuscula extus nitida glabraque margine bene ciliata, 0.6–0.7 mm. longa. Petala aestivatione quincuncialia oblonga sursum attenuata subacuta 2.8–3 mm. longa 1 mm. lata dimidia superiore parte minute hispidula. Stamina 10 glabra filamentis complanatis basi coalitis, parce papillosis longioribus 1.8–2 mm. longis brevioribus circa 1.4 mm. longis. Antherae 1 mm. longae, thecis oblongis infra lateralibus 0.4 mm. longis, connectivo crasse ovato sursum longe acuteque complanato-cuspidato. Discus 0.5 mm. altus squamis crassiusculis denticulatis coalitis. Ovarium glabrum ovoideum 5-loculare, in loculis ovule singulo. Stylus circa 0.5–0.7 mm. longus. Stigma capitatum 5-lobatum. Drupa sphaeroidea 15–20 mm. diamitens exocarpio laevi vel leviter granuloso 3–5 mm. crasso duplo, exteriori coriaceo compacto (in sicco) granuloso-resinoso, interno dense fibroso; endocarpio lignoso resinoso-lacunoso plus minusve tuberculato, 8–12 mm. diamitenti, 1–3 spermo. Epicarpium odore Cydoniae.

Type in the Herbarium of the Botanical Museum, Utrecht, Netherlands, collected in the Boschreserve Brownsberg in Surinam, June 28, 1924, by Reis (No. 64). Paratypes (flowering specimens) were collected in the Boschreserve Watramiri, Surinam, Boomnummer 1606, collected by the Forest Service, Boschwezen (No. 4720). in Botanical Museum, Utrecht, and in Instituto Agronomico do Norte, Belém do Pará.

Medium-size or large tree with brownish, lenticellate and glabrous terminal branchlets. Leaves thick-coriaceous, rigid, glabrous. Blade ovate-elliptic, ovate-oblong, oblong-elliptic or subobovate-lanceolate, suddenly acuminate or cuspidate at apex, rounded or obtuse at base and abruptly and shortly tapering into a broad petiole, 3–6 mm. long,

very thickened at base; 6–13 cm. long, 2.5–6 cm. broad; above lustrous, usually smooth, with prominulous and broad midrib, immersed secondary nerves and veins obsolete or more or less conspicuous; midrib very prominent beneath, 10–12 pairs of spreading secondary nerves thin, prominulous, near margin arcuate and anastomosing, reticulum minute and prominulous or sometimes immersed but conspicuous.

Inflorescences axillary and terminal, cymose-paniculate, dichotomous, shorter than leaves, peduncle 0.5–1.5 cm. long, stout, striate, more or less complanate, puberulous, branchlets short, angulate, minutely hispid-puberulous. Bracts amplexant, persistent, ovate, subacute, sparsely ciliate, 1.3–0.5 mm. long. Pedicels thick, glabrous, 0.4–0.5 mm. long. Sepals ovate, obtuse, rather thick, glabrous except for ciliate margin, 0.6–0.7 mm. long. Petals oblong, attenuate toward apex, subacute, 2.8–3 mm. long, 1 mm. broad, minutely hispidulous on upper half. Stamens 10, glabrous, filaments complanate, united at base, sparsely papillose, longer ones (1.8–2 mm.) alternating with 5 shorter (1.4 mm.). Anthers 1 mm. long, thecae narrowly oblong on lower sides, 0.4 mm. long, connective thick, ovate, compressed and acutely cuspidate at apex. Disk 0.5 mm. high, scales thick, denticulate, united. Ovary glabrous, ovoid, 5-locular, cells uniovulate. Style about 0.5–0.7 mm. long. Stigma capitate, 5-lobate. Drupe globose 15–20 mm. diameter, exocarp almost smooth or somewhat granular, 3–5 mm. thick and double, outer layer coriaceous, compact when dry, resinous-granular, inner layer densely fibrous; endocarp woody, resinous-lacunose, more or less tuberculate, 8–12 mm. diameter, 1–3 seeds. Epicarp with strong scent of *Cydonia* fruits.

S. cydonioides has been mistaken for *S. guianensis*, and it is difficult to distinguish in sterile specimens. But the fruit of *S. cydonioides* are very different; they have a double exocarp, the inner layer of which is fibrous and difficult to dissociate from the endocarp. The latter is more or less tuberculate; the hispid-puberulous petals also differentiate the two species.

S. cydonioides is a medium-size tree from the uninundatable rain forest ranging from Surinam to French Guiana and northeastern Brazil. Westward it spreads into the British and Venezuelan Guianas.

VENEZUELA: BOLÍVAR: El Dorado, 80–90 km. al sur, en selvas pluviales; árbol 20 m., drupas rojo-ladrillo, perfumadas, 15 mm., hojas discoloras; especie escasa, "trompillo," 30-III-1956, *Bernardi* 3033 (VEN).

BRITISH GUIANA: Cuyuni River, Akarabice Creek in mixed forest, tree 80 ft. high and 15 in. diameter, flowers green, "Duhuria," 28-VII-1933 (dry flowers), *Tutin* 421 (US, BM, U, paratype, flowers).

SURINAM: Boschreserve Watramiri, 21-VI-1920, *Boschwezen* 4720 (paratype, flowers US, IAN, U); 19-III-1919 *Boschwezen* 4296 (U); 8-X-1918, *Boschwezen* 4038 (US) (U); 6-V-1916, *Boschwezen* 1936 (U). Boschreserve Brownsberg, 28-VI-1924, *Boschwezen* 6495 (holotype, U). In montibus qui dicuntur Nassau; in bos bij km. 0.6 Boom 28 inch., 30 cm. dik; vrucht oranje, "Kwatta sirie" (Sur.), "soort buffelhout" (S-D.), *Lanjouw & Lindeman* 2194 (U). Awarraballi, Sectie O, XI-1944, *Stahel* 263 (A, NY, U).

FRENCH GUIANA: Crique Serpent Rive gauche à 800 m. de son embouchure; terrain marecageuse-sablonneuse; grains (fruit) de la grosseur d'un pois de couleur vert devenant brunâtre à maturité; "bofo-oudou" (Paramaka), 20-VII-1953, *BAFOG* 35M (P). Chantier Fosima à 1 km. au Sud de la sùcrú Margot, terrain plat et sain; fruits ronds 2-3 cm. jaun-orange à maturité ayant un odeur de pomme; "bofo-oudou" (Paramaka), "mahot-cochon" (nom commercial), 7-XII-1953, *BAFOG* 124M (P). Route de St. Laurent a Cayenne km. 18 coté droit et à 20 m. de la route s/terrain sain; fruits verts ronds 10-20 mm., pulpe 2-3 mm.; noyou très dur, odeur non définie; "boliquin" (Pamaka) "gris-gris rouge" (nom commercial); les rodins fendus en lamelles de 3 à 5 mm. d'épaisseur sur 10-12 cm. de largeur donnent les "gaulettes" qui servent à cloisonner les "carlets" habitations des établissements en forêts; 10-XII-1953, *BAFOG* 131M (P). St. Laurent, II-1956, "bofoudou" (Paramaka), *BAFOG* 347 (U). Route de Cayenne au km. 14.100 coté gauche et à 20 m. de la route; fruits jaunâtres, globuleux, 1.5-2 cm., odeur de pomme, groupes en grappes axillaires; "bofo-oudou" (Paramaka), "mahot cochon" ou "bois cochon" (noms commerciaux), 29-I-1957, *BAFOG* 7656 (U). "Herbier de la Guyane" Année 1863, *Melinon* s.n. (P). Cayenne, *Martin* s.n. (P, K).

BRAZIL: PARÁ: Trombetas, Rio Aminá, matta da terra firme a liste do Lago Salado, 22-IV-1917, *Ducke* 16809 (MG). Amapá, Rio Oiapoque, beira do rio, terra firme, alta; arvore de 6 m., fruto vermelho-salmon, 1-II-1950, *Fróes* 25783 (IAN). Amapá, Rio Oiapoque; terra firme, alta floresta alta arvore 15 m., 15-X-1950, *Fróes* 26636 (IAN).

Collections Cited

ABRAHAM, A. A.

- 152 *Humiria balsamifera* var. *floribunda*

ADJIMANG, E. O.

- 4849 *Sacoglottis gabonensis*

AFZELIUS, A.

- s.n. *Sacoglottis gabonensis*

ALLEMÃO, F., & CYSNEIROS, F.

- 255 *Humiria balsamifera* var. *floribunda*

ALLEN, P. H.

- 5812 *Humiriastrum diguense* subsp. *costaricense*
6415 *Vantanea barbourii*
6681 *Vantanea barbourii*

ALSTON, A. H. G., & LUTZ, B.

- 169 *Humiria balsamifera* var. *parvifolia*

ALTSON, R. A.

- 545 *Humiria balsamifera* var. *coriacea*

ANDERSON, C. W.

- 154 *Humiriastrum obovatum*
506 *Humiria balsamifera* var. *guianensis*
559 *Humiria balsamifera* var. *guianensis*

ANDERSON, M. J.

- s.n. *Humiriastrum dentatum*

APPUN, C. F.

- 37 *Humiria balsamifera* fma. *attenuata*

ARAQUE, J., & BARKLEY, F.

- 18Va021 *Humiria balsamifera* var. *subsessilis*

ARAUJO, J. M. P.

- 6 *Sacoglottis amazonica*

ARCHER, W. A.

- 7915 *Sacoglottis amazonica*
7964 *Sacoglottis amazonica*

ARISTEGUIETA, L.

- 2174 *Humiria balsamifera* var. *coriacea*

AUBLET, J. B. C. F.

- s.n. *Vantanea guianensis*

AUBREVILLE, A.

- 92 *Sacoglottis gabonensis*

BAFOG (BUREAU AGR. ET FORESTIER
GUYANAIS)

- 35M *Sacoglottis cydonioides*
48M *Vantanea parviflora* var. *parviflora*
102M *Vantanea parviflora* var. *parviflora*
124M *Sacoglottis cydonioides*
131M *Sacoglottis cydonioides*
220M *Vantanea parviflora* var. *parviflora*
228M *Humiria balsamifera* fma. *balsamifera*
247M *Vantanea parviflora* var. *parviflora*
347M *Sacoglottis cydonioides*
1083 *Humiria balsamifera* fma. *balsamifera*
7587 *Humiria balsamifera* fma. *balsamifera*
7622 *Sacoglottis guianensis* fma. *glabra*
7656 *Sacoglottis cydonioides*

BAILEY, I. W.

- 115 *Humiria balsamifera* fma. *balsamifera*

BAKER, B. O.

- s.n. *Endopleura uchi*
 58 *Endopleura uchi*
 9401 *Endopleura uchi*

BALDWIN, J.

- 3187 *Schistostemon oblongifolium*

BARBOSA DA SILVA, M.

- 73 *Humiria balsamifera* fma. *attenuata*

BARBOUR, W. R.

- 1018 *Vantanea barbourii*

BECCARI, N.

- s.n. *Humiria balsamifera* var. *guianensis*

BENA, P.

- 1319 *Humiriastrum excelsum*

BENOIST, R.

- 1239 *Humiria balsamifera* fma. *balsamifera*
 1530 *Vantanea guianensis*

BERNARDI, A. L.

- 1571 *Sacoglottis guianensis* fma. *guianensis*
 2601 *Humiria balsamifera* fma. *attenuata*
 2603 *Humiria balsamifera* var. *coriacea*
 2613 *Vantanea minor*
 2813 *Sacoglottis guianensis* fma. *guianensis*
 2814 *Humiriastrum obovatum*
 3033 *Sacoglottis cydonioides*
 38820 *Vantanea minor*

BLACK, G. A.

- 47-1001 *Endopleura uchi*
 47-1276 *Humiria balsamifera* fma. *balsamifera*
 47-1756 *Humiria balsamifera* var. *floribunda*
 48-2512 *Humiria balsamifera* var. *guianensis*
 48-2514 *Schistostemon retusum*
 48-2589 *Humiria balsamifera* var. *guianensis*

- 48-3249 *Humiria balsamifera* fma. *attenuata*

- 48-3453 *Sacoglottis mattogrossensis* fma. *glabra*

- 48-3555 *Sacoglottis guianensis* fma. *glabra*

- 49-8313 *Humiria balsamifera* fma. *balsamifera*

- 49-8369 *Humiria balsamifera* fma. *balsamifera*

- 50-8685 *Sacoglottis guianensis* fma. *glabra*

- 50-8831 *Sacoglottis guianensis* fma. *glabra*

- 50-9058 *Sacoglottis mattogrossensis* fma. *mattogrossensis*

- 51-12776 *Humiria balsamifera* fma. *attenuata*

- 51-13231 *Humiria balsamifera* fma. *balsamifera*

- 51-13454 *Sacoglottis guianensis* fma. *guianensis*

- 51-13843 *Sacoglottis mattogrossensis* fma. *mattogrossensis*

- 55-18577 *Humiria balsamifera* fma. *balsamifera*

- 57-19306 *Endopleura uchi*

BLACK, G. A., & FOSTER, M. B.

- 48-3393 *Sacoglottis amazonica*

BLACK, G. A., & LEDOUX, P.

- 50-10371 *Humiria balsamifera* var. *floribunda*

- 50-10553 *Sacoglottis guianensis* fma. *guianensis*

- 50-10783 *Humiriastrum cuspidatum* var. *cuspidatum*

BLACK, G. A., & MAGALHÃES, D.

- 51-11790 *Humiria balsamifera* var. *parvifolia*

- 51-12954 *Humiria balsamifera* fma. *balsamifera*

- 51-12972 *Sacoglottis guianensis* fma. *guianensis*

BLACK, G. A., EGLER, W., CAVALCANTE P., & SILVA, A.

- 57-19590 *Humiria balsamifera* var. *floribunda*

BLACK, G. A., FRÉES, R. L., &
LEDOUX, P.

- 50-9810 *Sacoglottis amazonica*
50-9811 *Humiriastrum excelsum*

BLANCHET, J. S.

- s.n. *Humiria balsamifera* var. *parvifolia*
85 *Vantanea compacta* var. *compacta*
1005 *Humiria balsamifera* var. *parvifolia*
2810 *Humiria balsamifera* var. *parvifolia*
3144A *Humiria floribunda* var. *parvifolia*
3305 *Vantanea compacta* var. *compacta*
3362 *Vantanea compacta* var. *compacta*
3422 *Humiria balsamifera* var. *parvifolia*
3570 *Humiria balsamifera* var. *parvifolia*
3805 *Vantanea compacta* var. *compacta*
3837 *Vantanea compacta* var. *compacta*

BOLDINGH, I.

- 3886 *Humiria balsamifera* var. *guianensis*

BOSCHWEZEN, B. W., SURINAM FOREST
SERVICE.

- 36A *Humiria balsamifera* var. *guianensis*
117 *Sacoglottis guianensis* fma. *guianensis*
177 *Humiria balsamifera* fma. *attenuata*
212 *Humiria balsamifera* fma. *balsamifera*
531 *Humiria balsamifera* fma. *guianensis*
1120 *Humiria balsamifera* var. *guianensis*
1166 *Sacoglottis guianensis* fma. *guianensis*
1490 *Sacoglottis guianensis* fma. *glabra*
1547 *Humiria balsamifera* fma. *balsamifera*
1935 *Humiria balsamifera* fma. *balsamifera*

- 1936 *Sacoglottis cydonioides*
2068 *Schistostemon densiflorum*
2232 *Humiria balsamifera* fma. *balsamifera*
2471 *Humiria balsamifera* fma. *balsamifera*
2599 *Humiria balsamifera* var. *guianensis*
2765 *Humiria balsamifera* fma. *balsamifera*
2816 *Humiria balsamifera* var. *guianensis*
2885 *Humiria balsamifera* fma. *balsamifera*
2918 *Humiria balsamifera* fma. *balsamifera*
2974 *Sacoglottis guianensis* fma. *guianensis*
3010 *Humiria balsamifera* fma. *balsamifera*
3040 *Humiria balsamifera* var. *guianensis*
3079 *Sacoglottis guianensis* fma. *guianensis*
3125 *Sacoglottis guianensis* fma. *guianensis*
3646 *Humiria balsamifera* var. *guianensis*
3934 *Humiria balsamifera* fma. *balsamifera*
3947 *Humiria balsamifera* var. *guianensis*
3961 *Sacoglottis guianensis* fma. *guianensis*
4038 *Sacoglottis cydonioides*
4296 *Sacoglottis cydonioides*
4469 *Sacoglottis guianensis* fma. *guianensis*
4669 *Humiria balsamifera* fma. *balsamifera*
4673 *Sacoglottis guianensis* fma. *guianensis*
4684 *Humiria balsamifera* fma. *balsamifera*
4720 *Sacoglottis cydonioides*
4770 *Humiria balsamifera* fma. *attenuata*
4810 *Humiria balsamifera* fma. *balsamifera*
4933 *Schistostemon densiflorum*
4960 *Schistostemon densiflorum*
5412 *Humiria balsamifera* fma. *balsamifera*

- 5430 *Sacoglottis guianensis* fma. *guianensis*
 5486 *Humiria balsamifera* var. *guianensis*
 5827 *Humiria balsamifera* fma. *balsamifera*
 5850 *Humiria balsamifera* fma. *attenuata*
 5858 *Humiria balsamifera* fma. *balsamifera*
 6010 *Humiria balsamifera* fma. *balsamifera*
 6068 *Humiria balsamifera* fma. *balsamifera*
 6234 *Humiria balsamifera* fma. *balsamifera*
 6495 *Sacoglottis cydonioides*
 6670 *Humiria balsamifera* fma. *balsamifera*
 6907 *Humiria balsamifera* fma. *balsamifera*

BRITTON, N. L.

- s.n. *Sacoglottis amazonica*

BROADWAY, W. E.

- 8475 *Sacoglottis amazonica*

BUCHTIEN, O.

- 1518 *Humiriastrum mapiriense*

BURGOS, J. A.

- 37 *Humiriastrum excelsum*

- 85 *Humiriastrum excelsum*

CAPUCHO, P.

- 430 *Endopleura uchi*

- 483 *Vantanea parviflora* var. *parviflora*

CARDONA, F.

- 774 *Humiria balsamifera* var. *coriacea*

- 965 *Humiria balsamifera* var. *guaiquinimana*

- 1112 *Humiria balsamifera* var. *guaiquinimana*

- 1768 *Humiria balsamifera* var. *coriacea*

- 1823 *Humiria balsamifera* var. *coriacea*

- 1869 *Humiria balsamifera* var. *coriacea*

- 1912 *Vantanea minor*

- 2269 *Humiria balsamifera* var. *coriacea*

- 2362 *Vantanea minor*

- 2533 *Humiria balsamifera* var. *coriacea*

- 2670 *Humiria balsamifera* var. *coriacea*

- 2877 *Humiria balsamifera* var. *coriacea*

CASARETTO, G.

- s.n. *Humiriastrum dentatum*

CHAGAS

- 3093 *Schistostemon macrophyllum*

CHAGAS & DIONISIO

- 3472 *Schistostemon macrophyllum*

COOPER, G. P.

- 68 *Sacoglottis gabonensis*

- 274 *Sacoglottis gabonensis*

COWAN, R. S.

- 38700 *Humiria balsamifera* fma. *balsamifera*

- 39263 *Humiria balsamifera* var. *guianensis*

- 39266 *Humiria balsamifera* var. *guianensis*

COWAN, R. S., & MAGUIRE, B.

- 38034 *Humiria balsamifera* var. *floribunda*

COWAN, R. S., & WURDACK, J. J.

- 31090 *Humiria balsamifera* var. *coriacea*

- 31301 *Humiria balsamifera* var. *coriacea*

- 31472 *Humiria balsamifera* var. *sessilis*

- 31502 *Humiria balsamifera* var. *sessilis*

- 32022 *Sacoglottis guianensis* fma. *guianensis*

CUATRECASAS, J.

- 7203 *Schistostemon retusum*

- 14418 *Humiriastrum diguense* var. *anchicayanum*

- 14956 *Humiriastrum diguense*

- 16615 *Humiriastrum procerum*
 17186 *Humiriastrum procerum*
 17226 *Sacoglottis ovicarpa*
 19727 *Humiria balsamifera* var. sub-
 sessilis
 19909 *Humiriastrum melanocarpum*
 19927 *Sacoglottis ovicarpa*
 19937 *Vantanea occidentalis*
 19989 *Humiriastrum melanocarpum*
 19998 *Sacoglottis ovicarpa*

CURRAN, H. M.

- 159 *Humiria balsamifera* var. parvi-
 folia

DAYTON, W. A., & BARBOUR, W. R.

- 3004 *Sacoglottis amazonica*
 3129 *Vantanea barbourii*

DE LA CRUZ, J. S.

- 2202 *Humiria balsamifera* var. gui-
 anensis
 2210 *Humiria balsamifera* var. gui-
 anensis
 2227 *Humiria balsamifera* var. gui-
 anensis
 2644 *Humiria balsamifera* var. gui-
 anensis
 2645 *Humiria balsamifera* var. gui-
 anensis

DINKLAGE, M. J.

- 2973 *Sacoglottis gabonensis*

DONANT HERB.

- 1686 *Humiria balsamifera* var. flori-
 bunda

DUCKE, A.

- s.n. *Sacoglottis amazonica*
 s.n. *Humiriastrum cuspidatum* var.
 cuspidatum
 s.n. *Endopleura uchi*
 12 *Sacoglottis ceratocarpa*
 16 *Sacoglottis ceratocarpa*
 16a *Sacoglottis ceratocarpa*
 87 *Humiria balsamifera* var. flori-
 bunda
 157 *Vantanea parviflora* var. parvi-
 flora
 200 *Vantanea guianensis*
 241 *Endopleura uchi*

- 243 *Humiriastrum cuspidatum* var.
 glabriflorum
 255 *Schistostemon macrophyllum*
 265 *Hylocarpa heterocarpa*
 305 *Endopleura uchi*
 363 *Sacoglottis mattogrossensis* fma.
 mattogrossensis
 416 *Vantanea macrocarpa*
 440 *Humiria balsamifera* var. flori-
 bunda
 519 *Sacoglottis mattogrossensis* fma.
 glabra
 541 *Humiria balsamifera* var. flori-
 bunda
 751 *Vantanea micrantha*
 752 *Vantanea paraensis*
 781 *Vantanea parviflora* var. parvi-
 flora
 1055 *Sacoglottis amazonica*
 1174 *Sacoglottis ceratocarpa*
 1175 *Schistostemon macrophyllum*
 1295 *Sacoglottis mattogrossensis* var.
 subintegra fma. subintegra
 1301 *Sacoglottis ceratocarpa*
 1513 *Vantanea compacta* var. com-
 pacta
 1614 *Humiriastrum excelsum*
 1647 *Vantanea guianensis*
 1723 *Sacoglottis amazonica*
 1744 *Schistostemon macrophyllum*
 1756 *Sacoglottis guianensis* var.
 maior
 2108 *Duckesia verrucosa*
 2188 *Sacoglottis mattogrossensis* fma.
 mattogrossensis
 2230 *Vantanea macrocarpa*
 7174 *Schistostemon macrophyllum*
 7213 *Humiria balsamifera* fma. at-
 tenuata
 8029 *Humiria balsamifera* var. flori-
 bunda
 8042 *Sacoglottis guianensis* fma. gui-
 anensis
 8368 *Sacoglottis guianensis* fma.
 guianensis
 8410 *Humiria balsamifera* var. gui-
 anensis
 8524 *Sacoglottis guianensis* fma.
 guianensis
 8628 *Humiriastrum cuspidatum* var.
 cuspidatum
 9123 *Humiria balsamifera* var. gui-
 anensis

- | | | | |
|-------|--|-------|--|
| 9866 | <i>Sacoglottis mattogrossensis</i> fma. glabra | 17780 | <i>Humiriastrum excelsum</i> |
| 9868 | <i>Sacoglottis guianensis</i> fma. glabra | 17781 | <i>Sacoglottis amazonica</i> |
| 10218 | <i>Sacoglottis mattogrossensis</i> fma. mattogrossensis | 17782 | <i>Vantanea paraensis</i> |
| 10815 | <i>Duckesia verrucosa</i> | 17783 | <i>Vantanea guianensis</i> |
| 11050 | <i>Sacoglottis mattogrossensis</i> fma. mattogrossensis | 17784 | <i>Sacoglottis guianensis</i> var. maior |
| 11550 | <i>Schistostemon macrophyllum</i> | 19166 | <i>Humiriastrum glaziovii</i> var. glaziovii |
| 11653 | <i>Sacoglottis mattogrossensis</i> fma. glabra | 20426 | <i>Vantanea parviflora</i> var. parviflora |
| 11790 | <i>Humiriastrum cuspidatum</i> var. cuspidatum | 20427 | <i>Vantanea macrocarpa</i> |
| 12030 | <i>Humiriastrum villosum</i> | 20428 | <i>Vantanea parviflora</i> var. parviflora |
| 12656 | <i>Sacoglottis guianensis</i> fma. glabra | 21024 | <i>Schistostemon macrophyllum</i> |
| 14872 | <i>Sacoglottis guianensis</i> fma. glabra | 21357 | <i>Vantanea macrocarpa</i> |
| 14962 | <i>Vantanea parviflora</i> var. parviflora | 23424 | <i>Humiria balsamifera</i> fma. balsamifera |
| 14967 | <i>Sacoglottis guianensis</i> fma. glabra | 23425 | <i>Vantanea parviflora</i> var. puberulifolia |
| 14979 | <i>Endopleura uchi</i> | 23426 | <i>Vantanea parviflora</i> var. parviflora |
| 14992 | <i>Duckesia verrucosa</i> | 23427 | <i>Vantanea parviflora</i> var. puberulifolia |
| 15234 | <i>Sacoglottis guianensis</i> fma. guianensis | 23428 | <i>Vantanea parviflora</i> var. puberulifolia |
| 15415 | <i>Vantanea guianensis</i> | 23429 | <i>Vantanea parviflora</i> var. parviflora |
| 15451 | <i>Vantanea guianensis</i> | 23430 | <i>Vantanea paraensis</i> |
| 15459 | <i>Humiriastrum excelsum</i> | 23431 | <i>Sacoglottis ceratocarpa</i> |
| 15467 | <i>Vantanea parviflora</i> var. parviflora | 23432 | <i>Schistostemon macrophyllum</i> |
| 15514 | <i>Humiria balsamifera</i> fma. balsamifera | 23433 | <i>Sacoglottis guianensis</i> var. maior |
| 15515 | <i>Humiria balsamifera</i> fma. balsamifera | 23434 | <i>Humiriastrum cuspidatum</i> var. cuspidatum |
| 16286 | <i>Sacoglottis mattogrossensis</i> var. subintegra fma. puberula | 23436 | <i>Humiriastrum cuspidatum</i> var. glabriflorum |
| 16320 | <i>Sacoglottis mattogrossensis</i> fma. mattogrossensis | 23814 | <i>Vantanea guianensis</i> |
| 16325 | <i>Duckesia verrucosa</i> | 23815 | <i>Endopleura uchi</i> |
| 16346 | <i>Sacoglottis mattogrossensis</i> fma. mattogrossensis | 23816 | <i>Schistostemon macrophyllum</i> |
| 16419 | <i>Sacoglottis guianensis</i> fma. guianensis | 23817 | <i>Schistostemon oblongifolium</i> |
| 16578 | <i>Sacoglottis amazonica</i> | 23818 | <i>Sacoglottis guianensis</i> var. maior |
| 16641 | <i>Endopleura uchi</i> | 23819 | <i>Schistostemon reticulatum</i> subsp. reticulatum |
| 16764 | <i>Duckesia verrucosa</i> | 23820 | <i>Sacoglottis mattogrossensis</i> var. subintegra fma. subintegra |
| 16809 | <i>Sacoglottis cydonioides</i> | 30126 | <i>Humiriastrum cuspidatum</i> var. cuspidatum |
| 17221 | <i>Sacoglottis amazonica</i> | 30128 | <i>Humiria balsamifera</i> fma. balsamifera |
| 17262 | <i>Sacoglottis mattogrossensis</i> fma. glabra | 30131 | <i>Schistostemon retusum</i> |
| 17779 | <i>Endopleura uchi</i> | 30133 | <i>Vantanea macrocarpa</i> |
| | | 30134 | <i>Vantanea tuberculata</i> |

- 30135 *Vantanea micrantha*
 30137 *Hylocarpa heterocarpa*

DUCKE, A., & KUHLMANN, J. G.

- 19165 *Sacoglottis mattogrossensis*
 fma. *mattogrossensis*

EDWARDSON, I. E.

- 181 *Sacoglottis gabonensis*

EGLER, W. A.

- 261 *Humiria balsamifera* var. *floribunda*
 281 *Sacoglottis guianensis* fma. *glabra*

FANSHAVE, D. B.

- F715 *Humiria balsamifera* fma. *balsamifera*

FERNANDEZ, A.

- 2084 *Humiria balsamifera* var. *laurina*
 2142 *Schistostemon retusum*
 2148 *Humiria balsamifera* var. *guianensis*
 2228 *Sacoglottis mattogrossensis* fma. *glabra*

FOCKE, H. C.

- 1018 *Humiria balsamifera* var. *guianensis*
 1286 *Humiria balsamifera* var. *guianensis*

FOREST DEPARTMENT, BRITISH GUIANA

- 154 *Humirastrum obovatum*
 404A *Schistostemon densiflorum*
 506 *Humiria balsamifera* var. *guianensis*
 559 *Humiria balsamifera* var. *guianensis*
 600 *Vantanea guianensis*
 663 *Humiria balsamifera* var. *laurina*
 931 *Humirastrum obovatum*
 2055 *Humiria balsamifera* var. *guianensis*

FRAZÃO, A.

- 8118 *Sacoglottis mattogrossensis* fma. *mattogrossensis*

FRÓES, R. L.

- 11813 *Humiria balsamifera* var. *floribunda*
 19933 *Vantanea obovata*
 20480 *Humiria balsamifera* var. *floribunda*
 20803 *Humirastrum cuspidatum* var. *glabriflorum*
 21090 *Schistostemon oblongifolium*
 21192 *Sacoglottis ceratocarpa*
 21338 *Humiria balsamifera* var. *guianensis*
 21342 *Humiria balsamifera* var. *guianensis*
 21346 *Humiria balsamifera* var. *floribunda*
 21370 *Schistostemon reticulatum* subsp. *froesii*
 21411 *Schistostemon retusum*
 21437 *Schistostemon oblongifolium*
 22472 *Schistostemon macrophyllum*
 22587 *Sacoglottis guianensis* var. *hispidula*
 22644 *Humirastrum villosum*
 22703 *Schistostemon macrophyllum*
 22738 *Humiria balsamifera* fma. *attenuata*
 22747 *Schistostemon retusum*
 22760 *Humiria balsamifera* var. *guianensis*
 22838 *Humiria balsamifera* var. *guianensis*
 22842 *Humiria balsamifera* var. *guianensis*
 22857 *Sacoglottis guianensis* fma. *guianensis*
 22940 *Sacoglottis guianensis* fma. *guianensis*
 23494 *Sacoglottis guianensis* fma. *glabra*
 24256 *Sacoglottis mattogrossensis* fma. *mattogrossensis*
 24297 *Sacoglottis mattogrossensis* fma. *mattogrossensis*
 24820 *Humirastrum cuspidatum* var. *subhirtellum*
 24916 *Schistostemon macrophyllum*
 24924 *Humirastrum piraparanense*
 24934 *Sacoglottis ceratocarpa*
 24936 *Vantanea guianensis*
 25185 *Vantanea parviflora* var. *parviflora*

- 25369 *Sacoglottis guianensis* var.
hispidula
25438 *Humiriastrum cuspidatum*
var. *cuspidatum*
25459 *Vantanea parviflora* var. *par-*
viflora
25463 *Humiriastrum cuspidatum*
var. *subhirtellum*
25480 *Humiriastrum cuspidatum* var.
subhirtellum
25565 *Endopleura uchi*
25783 *Sacoglottis cydonioides*
26071 *Schistostemon macrophyllum*
26428 *Vantanea paraensis*
26636 *Sacoglottis cydonioides*
26812 *Humiria balsamifera* var. *flori-*
bunda
27985 *Humiriastrum piraparanense*
28407 *Humiriastrum piraparanense*
28454 *Humiria balsamifera* fma. *at-*
tenuata
28895 *Humiria balsamifera* fma. *at-*
tenuata
29854 *Humiria balsamifera* fma. *bal-*
samifera
30093 *Humiria balsamifera* var. *flori-*
bunda
30284 *Sacoglottis guianensis* fma. *gui-*
anensis
30416 *Sacoglottis mattogrossensis*
fma. *subintegra*
30670 *Sacoglottis guianensis* fma. *glab-*
ra
32391 *Sacoglottis mattogrossensis*
fma. *mattogrossensis*
32478 *Sacoglottis guianensis* fma.
glabra

FRÓES, R. L., & ADDISON, G.

- 29096 *Humiria balsamifera* var. *gui-*
anensis
29102 *Humiria balsamifera* var. *gui-*
anensis
29119 *Schistostemon macrophyllum*
29144 *Humiriastrum villosum*
29211 *Humiria balsamifera* var. *gui-*
anensis

FRÓES, R. L., & BLACK, G. A.

- 27572 *Humiria balsamifera* var. *flori-*
bunda

FRÓES, R. L., & FILHO, J. P.

- 29486 *Humiria balsamifera* fma. *bal-*
samifera

GARCÍA BARRIGA, H.

- 13681 *Sacoglottis guianensis* fma.
glabra
14287 *Humiriastrum piraparanense*

GARDNER, C. A.

- 1146 *Sacoglottis mattogrossensis* fma.
glabra
1263 *Humiria balsamifera* var. *flori-*
bunda
4452 *Vantanea obovata*
4452 bis *Humiria balsamifera* var. *mi-*
narum

GLAZIOU, A. F. M.

- s.n. *Humiria balsamifera* var. *parvi-*
folia
63 *Humiria balsamifera* var. *parvi-*
folia
731 *Humiria balsamifera* var. *parvi-*
folia
6196 *Humiria balsamifera* var. *parvi-*
folia
7765 *Humiria balsamifera* var. *parvi-*
folia
8286 *Humiria balsamifera* var. *parvi-*
folia
10078 *Vantanea guianensis*
10342 *Humiria balsamifera* var. *par-*
vifolia
10437 *Humiria balsamifera* var. *flori-*
bunda
11828 *Vantanea compacta* var. *com-*
pacta
11829 *Vantanea compacta* var. *com-*
pacta
12515 *Humiria floribunda* var. *parvi-*
folia
14640 *Vantanea compacta* var. *gran-*
diflora
16723 *Vantanea compacta* var. *gran-*
diflora
16724 *Humiriastrum glaziovii* var.
angustifolium
18178 *Humiriastrum dentatum*
18179 *Humiriastrum glaziovii* var.
glaziovii

- 18180 *Humiria balsamifera* var. *parvifolia*
 18181 *Vantanea compacta* var. *grandiflora*
 18182 *Vantanea compacta* var. *compacta*
 18962 *Humiria balsamifera* var. *parvifolia*
 18963 *Vantanea obovata*
 18964 *Humiriastrum glaziovii* var. *glaziovii*

GLEASON, H. A.

- 729 *Humiriastrum obovatum*

GOMES, A. I.

- s.n. *Humiria balsamifera* var. *parvifolia*

GOSSEWEILER, J.

- 751 *Sacoglottis gabonensis*
 6996 *Sacoglottis gabonensis*
 8182 *Sacoglottis gabonensis*
 8707 *Sacoglottis gabonensis*
 8751 *Sacoglottis gabonensis*

GUEDES, M.

- 1260 *Endopleura uchi*

GUEDES, T.

- 58 *Sacoglottis ceratocarpa*
 80 *Sacoglottis ceratocarpa*

GUILDING, L.

- s.n. *Sacoglottis amazonica*

GUILLEMIN, A.

- 205 *Humiria balsamifera* var. *parvifolia*

GUPPY, N.

- 308 *Sacoglottis amazonica*

HART, J. H.

- s.n. *Sacoglottis amazonica*

HITCHCOCK, A. E.

- 16938 *Humiria balsamifera* var. *guianensis*

HOEHNE, F. C.

- 3021 *Humiriastrum glaziovii* var. *angustifolium*

- 7970 *Humiria balsamifera* var. *parvifolia*

- 29281 *Vantanea compacta* var. *compacta*

HOSTMAN, W. R.

- 793 *Humiria balsamifera* var. *guianensis*

HOUTMONSTER

- 541A *Humiria balsamifera* fma. *balsamifera*

- 542A *Humiria balsamifera* fma. *balsamifera*

- 543A *Humiria balsamifera* fma. *balsamifera*

HUBER, H.

- 96 *Humiria balsamifera* var. *floribunda*

- 239 *Endopleura uchi*

- 940 *Endopleura uchi*

- 1260 *Endopleura uchi*

- 1850 *Sacoglottis amazonica*

- 2785 *Humiria balsamifera* fma. *balsamifera*

- 6992 *Sacoglottis mattogrossensis* fma. *glabra*

- 9583 *Vantanea parviflora* var. *parviflora*

- 10446 *Sacoglottis guianensis* fma. *guianensis*

HUMBERT, H.

- 27422 *Humiria balsamifera* var. *subsessilis*

- 27440 *Humiria balsamifera* var. *guianensis*

HUMBERT, H., & SCHULTES, R. E.

- 27363 *Humiriastrum villosum*

- 27364 *Humiria balsamifera* fma. *subsessilis*

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- 86 *Humiria balsamifera* var. *floribunda*

- 204 *Humiriastrum cuspidatum* var. *glabriflorum*

- 244 *Schistostemon macrophyllum*

- 620 *Humiria balsamifera* var. *coriacea*

- 1056 *Humiria balsamifera* var. *floribunda*
 1243 *Schistostemon macrophyllum*
 1407 *Schistostemon macrophyllum*
 1638 *Sacoglottis ceratocarpa*
 1684 *Humiria balsamifera* var. *guianensis*
 1700 *Humirastrum cuspidatum* var. *glabriflorum*
 1773 *Humiria balsamifera* var. *floribunda*
 1809 *Vantanea parviflora* var. *parviflora*
 1814 *Sacoglottis ceratocarpa*
 2044 *Schistostemon macrophyllum*
 2084 *Sacoglottis ceratocarpa*
 IRWIN, H. S.
 246 *Humiria balsamifera* fma. *attenuata*
 JENMAN, G. S.
 287 *Schistostemon densiflorum*
 299 *Humiria balsamifera* var. *guianensis*
 478 *Schistostemon densiflorum*
 1023 *Humiria balsamifera* var. *coriacea*
 1281 *Humiria balsamifera* var. *guianensis*
 2489 *Schistostemon densiflorum*
 3912 *Humiria balsamifera* fma. *balsamifera*
 4719 *Schistostemon densiflorum*
 4883 *Humiria balsamifera* var. *guianensis*
 5561 *Humiria balsamifera* var. *guianensis*
 5562 *Humiria balsamifera* var. *guianensis*
 5672 *Humiria balsamifera* fma. *balsamifera*
 s.n. *Humirastrum obovatum*
 JOBERT, Dr.
 362 *Vantanea guianensis*
 JUNKER, N. W.
 5525 *Humiria balsamifera* fma. *balsamifera*
 KAPPLER, A.
 s.n. *Schistostemon dichotomum*
 2144 *Schistostemon dichotomum*
 KILLIP, E. P., & SMITH, A. C.
 28681 *Humiria balsamifera* fma. *attenuata*
 KLEIN, R.
 37b *Vantanea compacta* var. *compacta*
 KLUG, G.
 1091 *Vantanea peruviana*
 1130 *Vantanea peruviana*
 1315 *Humiria balsamifera* fma. *attenuata*
 1564 *Schistostemon reticulatum* subsp. *reticulatum*
 2846 *Humiria balsamifera* fma. *attenuata*
 3706 *Humiria balsamifera* var. *parvifolia*
 KOECHLIN, J.
 2632 *Sacoglottis gabonensis*
 KRUKOFF, B.
 121 *Sacoglottis gabonensis*
 1483 *Humiria balsamifera* var. *laurina*
 4956 *Vantanea parviflora* var. *parviflora*
 6371 *Vantanea celativenia*
 6506 *Sacoglottis amazonica*
 6653 *Sacoglottis guianensis* var. *hispidula*
 7082 *Sacoglottis guianensis* fma. *guianensis*
 7120 *Vantanea parviflora* var. *parviflora*
 7182 *Vantanea celativenia*
 7926 *Humiria balsamifera* var. *floribunda*
 7928 *Humiria balsamifera* var. *floribunda*
 8757 *Sacoglottis guianensis* fma. *glabra*
 11270 *Humirastrum mapiriense*
 KUHLMAN, J. G.
 2128 *Sacoglottis mattogrossensis* fma. *mattogrossensis*
 2894 *Humiria balsamifera* var. *guianensis*
 3509 *Humiria balsamifera* var. *floribunda*

- 3510 *Sacoglottis guianensis* var. *hispidula*
 21029 *Schistostemon macrophyllum*

KUYPPER, J.

- 33 *Humiria balsamifera* var. *guianensis*
 568 *Humiria balsamifera* var. *guianensis*

LAMB, F. B.

- 133 *Vantanea magdalenensis*
 141 *Humirastrum colombianum*
 145 *Humirastrum colombianum*
 170 *Humirastrum colombianum*

LANJOUW, J.

- 195 *Humiria balsamifera* var. *guianensis*
 334 *Humiria balsamifera* var. *guianensis*
 1253 *Humiria balsamifera* fma. *balsamifera*

LANJOUW, J., & LINDEMAN, J. C.

- H8 *Humiria balsamifera* fma. *balsamifera*
 267 *Humiria balsamifera* var. *guianensis*
 268 *Humiria balsamifera* var. *guianensis*
 573 *Humiria balsamifera* fma. *balsamifera*
 652 *Humiria balsamifera* fma. *balsamifera*
 911 *Humiria balsamifera* var. *guianensis*
 968 *Humiria balsamifera* var. *floribunda*
 1797 *Humiria balsamifera* var. *guianensis*
 1798 *Humiria balsamifera* var. *guianensis*
 2194 *Sacoglottis cydonioides*
 2869 *Sacoglottis guianensis* fma. *guianensis*
 3259 *Humiria balsamifera* var. *guianensis*
 3289 *Humiria balsamifera* var. *guianensis*
 3317 *Humiria balsamifera* var. *guianensis*

LASSER, T., & VARESCHI, V.

- 3888 *Humiria balsamifera* var. *coriacea*

LEBLOND

- 402 *Humiria balsamifera* var. *floribunda*
 441 *Humiria balsamifera* var. *floribunda*

LE PRIEUR, M.

- 253 *Sacoglottis guianensis* fma. *guianensis*
 1838 *Humiria balsamifera* fma. *balsamifera*
 1840 *Humiria balsamifera* fma. *balsamifera*

LIMA, D. DE

- 1623 *Humiria balsamifera* var. *parvifolia*
 49-336 *Sacoglottis mattogrossensis* fma. *glabra*
 53-1273 *Humiria balsamifera* fma. *attenuata*
 53-1332 *Sacoglottis mattogrossensis* fma. *glabra*

LINDEMAN, J. C.

- 258 *Humiria balsamifera* var. *guianensis*
 4201 *Humiria balsamifera* var. *floribunda*
 4202 *Humiria balsamifera* fma. *balsamifera*
 4381 *Humiria balsamifera* var. *guianensis*
 6541 *Humiria balsamifera* fma. *balsamifera*
 6861 *Humiria balsamifera* fma. *balsamifera*
 6862 *Humiria balsamifera* var. *floribunda*
 6880 *Humiria balsamifera* fma. *balsamifera*
 6881 *Humiria balsamifera* var. *guianensis*
 6882 *Humiria balsamifera* var. *guianensis*

6883 *Humiria balsamifera* var. *guianensis*

LISBOA, A.

2327 *Humiria balsamifera* var. *floribunda*

2327 *Humiria balsamifera* var. *laurina*

2330 *Sacoglottis guianensis* var. *maior*

4099 *Humiria balsamifera* var. *floribunda*

LITTLE, E. L.

6233 *Humiriastrum procerum*

6320 *Humiriastrum procerum*

6412 *Humiriastrum procerum*

6413 *Humiriastrum procerum*

LUETZELBURG, P. v.

40 *Vantanea obovata*

22561 *Humiria balsamifera* var. *guianensis*

22575 *Humiria balsamifera* var. *guianensis*

22627 *Humiria balsamifera* var. *guianensis*

24014 *Humiria balsamifera* var. *subsessilis*

LUNT, W.

s.n. *Sacoglottis amazonica*

5984 *Sacoglottis amazonica*

LUTZ, B.

681 *Humiria balsamifera* var. *parvifolia*

MACEDO, A.

3922 *Sacoglottis guianensis* fma. *guianensis*

4034 *Humiria balsamifera* fma. *attenuata*

MAGUIRE, B.

24223 *Humiria balsamifera* var. *coriacea*

24443 *Humiria balsamifera* var. *coriacea*

24707 *Humiria balsamifera* var. *coriacea*

24789 *Humiria balsamifera* var. *coriacea*

24836 *Sacoglottis guianensis* var. *hispidula*

24844 *Sacoglottis guianensis* fma. *guianensis*

29337 *Sacoglottis guianensis* var. *hispidula*

32686 *Humiria balsamifera* var. *coriacea*

32763 *Humiria balsamifera* var. *guaiquinimana*

33099 *Humiria balsamifera* var. *guaiquinimana*

33242 *Humiria balsamifera* var. *iluana*

33388 *Humiria balsamifera* var. *iluana*

MAGUIRE, B., & FANSHAWE, D. B.

23233 *Humiria crassifolia*

23295 *Humiria balsamifera* var. *coriacea*

23450 *Humiria balsamifera* var. *guianensis*

32158 *Humiria balsamifera* var. *imbaimadaiensis*

MAGUIRE, B., & MAGUIRE, C.

35040 *Humiria balsamifera* var. *floribunda*

35140 *Humiria balsamifera* var. *coriacea*

35453 *Humiria balsamifera* var. *coriacea*

40105 *Humiria balsamifera* var. *stenocarpa*

40159 *Humiria balsamifera* var. *coriacea*

MAGUIRE, B., & POLITI, L.

27627 *Humiria balsamifera* var. *coriacea*

27695 *Humiria balsamifera* var. *coriacea*

27974 *Humiria balsamifera* var. *floribunda*

28828 *Humiria balsamifera* var. *guianensis*

MAGUIRE, B., & STAHEL, G.

23654 *Humiria balsamifera* var. *guianensis*

23696 *Humiria balsamifera* var. *guianensis*

24957 *Humiria balsamifera* fma.
attenuata

MAGUIRE, B., & WURDACK, J. J.

34677 *Humiria balsamifera* var.
laurina

35579 *Humiria balsamifera* var.
laurina

MAGUIRE, B., COWAN, R. S., &
WURDACK, J. J.

29416 *Sacoglottis guianensis* var. his-
pidula

29416A *Humiria balsamifera* var.
subsessilis

29541 *Humiria balsamifera* var.
coriacea

29697 *Humiria balsamifera* var.
coriacea

29769 *Humiria balsamifera* var.
subsessilis

30018 *Humiria balsamifera* var.
coriacea

30483 *Humiria fruticosa*

30543 *Humiria balsamifera* var.
guianensis

30561 *Humiria fruticosa*

30622 *Humiria balsamifera* var.
coriacea

30693 *Sacoglottis maguirei*

30791 *Humiria balsamifera* var.
guianensis

30844 *Sacoglottis guianensis* fma.
guianensis

30885 *Humiria balsamifera* var.
coriacea

30918 *Humiria balsamifera* var.
coriacea

30967 *Sacoglottis guianensis* fma.
guianensis

30987 *Humiria balsamifera* var.
floribunda

MAGUIRE, B., WURDACK, J. J., &
BUNTING, G.

35882 *Humiria balsamifera* var.
stenocarpa

36210 *Humiria balsamifera* var.
subsessilis

36295 *Humiria balsamifera* var.
guianensis

36354 *Humiria balsamifera* var.
laurina

36456 *Humiria balsamifera* var.
guianensis

36580 *Humiria fruticosa*

37632 *Humiria balsamifera* var.
laurina

MAGUIRE, B., WURDACK, J. J., &
KEITH, W.

41821 *Humiria balsamifera* var.
laurina

41917 *Humiria balsamifera* var.
guianensis

MAGUIRE, B., WURDACK, J. J., &
MAGUIRE, C.

41640 *Vantanea guianensis*

MALME, G. D.

2237 *Sacoglottis mattogrossensis*
fma. mattogrossensis

MANN, G.

925 *Sacoglottis gabonensis*

1417 *Sacoglottis gabonensis*

MARTIN, J.

s.n. *Humiria balsamifera* fma. balsa-
mifera

s.n. *Humiriastrum subcrenatum*

s.n. *Sacoglottis cydonioides*

MARTIUS, C. E. P.

s.n. *Humiria balsamifera* fma. atte-
nuata

s.n. *Humiria balsamifera* var. flori-
bunda

s.n. *Humiria crassifolia*

s.n. *Humiriastrum cuspidatum* var.
cuspidatum

s.n. *Sacoglottis amazonica*

s.n. *Vantanea obovata*

MARTYN, E. B.

136 *Humiria balsamifera* var. gui-
anensis

MELINON, M.

s.n. *Humiria balsamifera* fma. bal-
samifera

s.n. *Sacoglottis cydonioides*

s.n. *Sacoglottis guianensis* fma. gla-
bra

- s.n. *Sacoglottis guianensis* fma. *guianensis*
s.n. *Vantanea parviflora* var. *parviflora*
48 *Humiria balsamifera* fma. *balsamifera*
100 *Vantanea guianensis* (US)
100 *Vantanea parviflora* var. *parviflora* (P, BM)
377 *Humiria balsamifera* fma. *balsamifera*
584 *Sacoglottis guianensis* fma. *guianensis*

MELLO FILHO, L. E.

- 1186 *Humiria balsamifera* var. *parvifolia*

MENDES MAGALHÃES

- 2117 *Vantanea obovata*

MERKER, C. A., SCHOLTES, J. A., &
DAYTON, W. A.

- 3041 *Sacoglottis amazonica*

MEXIA, Y.

- 5815 *Humiria balsamifera* var. *minorum*
6049 *Vantanea guianensis*

MIERS, J.

- 6167 *Vantanea parviflora* var. *parviflora*
8915 *Humiria balsamifera* var. *parvifolia*

MONTES DA COSTA

- 281 *Sacoglottis guianensis* var. *maior*

MOSÉN, H.

- 3475 *Humirastrum dentatum*
3477 *Sacoglottis* *mattogrossensis*
fma. *glabra*

MOSS, M.

- 13 *Humiria balsamifera* fma. *balsamifera*
57 *Humiria balsamifera* fma. *balsamifera*

MUSEU GOELDI

- 1260 *Endopleura uchi*
9419 *Humiria balsamifera* fma. *balsamifera*

- 9583 *Vantanea parviflora* var. *parviflora*
9664 *Vantanea guianensis*
9670 *Vantanea parviflora* var. *parviflora*
9672 *Humirastrum excelsum*
9680 *Vantanea parviflora* var. *parviflora*
9723 *Vantanea parviflora* var. *parviflora*
10130 *Sacoglottis mattogrossensis*
fma. *glabra*

OIGNE, C.

- 2800 *Sacoglottis gabonensis*

PATIÑO, V. M.

- 12 *Vantanea occidentalis*

PEARCE, R.

- s.n. *Vantanea compacta* subsp. *microcarpa*

PERSAUD, A. C.

- 102 *Schistostemon densiflorum*
191 *Humiria balsamifera* fma. *attenuata*
288 *Schistostemon densiflorum*

PHELPS, K., & HITCHCOCK, C.

- 508 *Humiria balsamifera* var. *coriacea*

PICKEL, D. B.

- 591 *Sacoglottis mattogrossensis* fma. *glabra*

PIRES, J. MURÇA

- s.n. *Vantanea parviflora* var. *parviflora*
41 *Sacoglottis guianensis* fma. *guianensis*
588 *Schistostemon oblongifolium*
708 *Hylocarpa heterocarpa*
754 *Humiria balsamifera* var. *guianensis*
989 *Humiria balsamifera* fma. *balsamifera*
1029 *Humiria balsamifera* var. *subsessilis*
1030 *Humirastrum piraparanense*

- 1510 *Sacoglottis mattogrossensis* fma. *mattogrossensis* POITEAU, A.
 3877 *Humiria balsamifera* var. *laurina* s.n. *Humiria balsamifera* fma. *attenuata*
- 4017 *Sacoglottis mattogrossensis* fma. *mattogrossensis* PULLE, A.
 4518 *Vantanea guianensis* 52 *Humiria balsamifera* var. *guianensis*
 PIRES, J. M., & BLACK, G. A. 150 *Humiria balsamifera* var. *guianensis*
 31 *Sacoglottis amazonica*
 2961 *Humiria balsamifera* var. *parvifolia* RAMAGE, G. A.
 PIRES, J. M., & SILVA, A. s.n. *Sacoglottis mattogrossensis* fma. *glabra*
- 4192 *Humiria balsamifera* var. *floribunda* RAMOS, G., & PATIÑO, V. M.
 4624 *Humiria balsamifera* fma. *attenuata* s.n. *Vantanea occidentalis*
 4629 *Humiria balsamifera* fma. *attenuata* RECH, DR.
 4702 *Humiria balsamifera* var. *floribunda* 1862 *Schistostemon dichotomum*
- PIRES, J. M., BLACK, G. A., WURDACK, J. J., & NILO REITZ, P. R.
 6140 *Sacoglottis mattogrossensis* fma. *mattogrossensis* 3353 *Vantanea compacta* var. *compacta*
 PIRES, J. M., BLACK, G. A., WURDACK, J. J., & SILVA, A. REITZ, P. R., & KLEIN, R.
 6209 *Humiria balsamifera* var. *laurina* 1589 *Vantanea compacta* var. *compacta*
 PIRES, J. M., FRÓES, R. L., & SILVA, A. 1730 *Vantanea compacta* var. *compacta*
 4954 *Vantanea parviflora* var. *parviflora* 1744 *Vantanea compacta* var. *compacta*
 5105 *Vantanea parviflora* var. *parviflora* 1836 *Vantanea compacta* var. *compacta*
 5380 *Vantanea guianensis* RICHARD, L. C.
 PITTIER, H. s.n. *Humiria balsamifera* fma. *balsamifera*
 16260 *Sacoglottis ovicarpa* s.n. *Humiria balsamifera* var. *floribunda*
 POEPPIG, E. s.n. *Humiria balsamifera* var. *parvifolia*
 s.n. *Humiria balsamifera* var. *floribunda* s.n. *Humiriastrum dentatum*
 18 *Humiria balsamifera* var. *floribunda* s.n. *Vantanea parviflora* var. *parviflora*
 3011 *Humiria balsamifera* var. *floribunda* RIEDEL, L.
 s.n. *Humiria balsamifera* var. *floribunda*
 s.n. *Humiria balsamifera* var. *minarum*
 s.n. *Humiria balsamifera* var. *parvifolia*

- s.n. *Humiriastrum glaziovii* var.
glaziovii
s.n. *Sacoglottis guianensis* fma. gui-
anensis
3570 *Humiria balsamifera* var. parvi-
folia

ROMBOUTO, H. E.

- 228 *Humiria balsamifera* fma. at-
tenuata

ROMERO CASTAÑEDA, R.

- 4785 *Humiriastrum colombianum*
4942 *Humiriastrum colombianum*

RUDGE, E.

- s.n. *Humiria balsamifera* fma. bal-
samifera

SAGOT, P. A.

- s.n. *Humiria balsamifera* fma. bal-
samifera

ST. HILAIRE, A. DE

- s.n. *Humiria balsamifera* var. parvi-
folia
114/5 *Humiria balsamifera* var. par-
vifolia
1705 *Vantanea obovata*
1984 bis *Vantanea obovata*

SALZMAN, P.

- s.n. *Humiria balsamifera* var. flori-
bunda

SAMUELS, J. A.

- s.n. *Humiria balsamifera* var. gui-
anensis

SANDEMAN, CHRISTOPHER

- 2199 *Humiria balsamifera* var. gui-
anensis

SANDWITH, N. Y.

- 374 *Schistostemon densiflorum*
399 *Humiria balsamifera* fma. bal-
samifera

SCHOMBURGK, R.

- 47 *Vantanea guianensis*
135 *Humiriastrum obovatum*
166 *Humiriastrum obovatum*

- 270 *Humiria balsamifera* var. gui-
anensis
346 *Humiria balsamifera* var. laurina
543 *Schistostemon densiflorum*
560 *Humiria balsamifera* var. laurina
571 *Sacoglottis guianensis* fma. gui-
anensis
574 *Sacoglottis guianensis* fma. gui-
anensis
576 *Humiria balsamifera* var. savan-
narum
584 *Humiriastrum obovatum*
628 *Humiria balsamifera* var. laurina
825 *Humiriastrum obovatum*
842 *Sacoglottis guianensis* fma. gui-
anensis
845 *Humiria balsamifera* var. savan-
narum
968 *Humiria balsamifera* var. laurina
982 *Vantanea guianensis*
1359 *Humiriastrum obovatum*
1552 *Vantanea minor*
1581 *Vantanea guianensis*
s.n. *Humiria balsamifera* var. laurina

SCHULTES, R. E.

- 9431a *Humiria balsamifera* fma. bal-
samifera
9435 *Humiria balsamifera* fma. balsa-
mifera
23131 *Humiriastrum cuspidatum* var.
cuspidatum

SCHULTES, R. E., & CABRERA, I.

- 15054 *Humiria crassifolia*
15511 *Humiria balsamifera* fma. at-
tenuata
15922 *Humiriastrum piraparanense*
16893 *Humiria balsamifera* fma.
attenuata
17045 *Sacoglottis ceratocarpa*
17231 *Humiria balsamifera* var. sub-
sessilis
17253 *Sacoglottis ceratocarpa*
18319 *Humiria balsamifera* var. sub-
sessilis
18371 *Humiria balsamifera* var. sub-
sessilis
19290a *Sacoglottis ceratocarpa*
19519 *Sacoglottis ceratocarpa*
19951 *Humiria balsamifera* var.
laurina

- 19963 *Humiria balsamifera* var. *laurina*

SCHULTES, R. E., & LÓPEZ, F.

- 8881 *Schistostemon macrophyllum*
 9267 *Vantanea parviflora* var. *parviflora*
 9363 *Humiria balsamifera* var. *guianensis*
 9510 *Humiria balsamifera* var. *sessilis*
 9701 *Humiriastrum cuspidatum* var. *cuspidatum*
 10339 *Humiria balsamifera* var. *floribunda*

SCHULTES, R. E., & PIRES, J. M.

- 9103A *Humiria balsamifera* var. *sessilis*

SEGADAS-VIANNA, F.

- 3506 *Humiria balsamifera* var. *parvifolia*
 3634 *Humiria balsamifera* var. *parvifolia*
 3635 *Humiria balsamifera* var. *parvifolia*

SEGADAS-VIANNA, F., DAU, L.,
 ORMOND, W. T., MACHLINE,
 G. C., & LOREDO, L.

- I-310 and I-369 *Humiria balsamifera* var. *parvifolia*
 I-385 *Humiria balsamifera* var. *parvifolia*
 I-439 *Humiria balsamifera* var. *parvifolia*
 I-821 *Humiria balsamifera* var. *parvifolia*
 I-907 *Humiria balsamifera* var. *parvifolia*
 I-945 *Humiria balsamifera* var. *parvifolia*
 I-1383 *Humiria balsamifera* var. *parvifolia*
 I-1416 *Humiria balsamifera* var. *parvifolia*

SELLOW, F.

- s.n. *Humiria balsamifera* var. *floribunda*
 s.n. *Humiria balsamifera* var. *parvifolia*

- 171 *Humiria balsamifera* var. *floribunda*

- 180 *Humiria balsamifera* var. *parvifolia*

- 2212 *Humiria balsamifera* var. *parvifolia*

- 2228 *Humiria balsamifera* var. *parvifolia*

SILVA, A.

- 59 *Sacoglottis mattogrossensis* fma. *glabra*

SILVA, J. F.

- 416 *Duckesia verrucosa*

SIQUEIRA, R.

- 8281 *Sacoglottis guianensis* var. *major*

- 8775 *Vantanea guianensis*

SMITH, A. C.

- 2176 *Humiria balsamifera* var. *guianensis*

- 2423 *Humiria balsamifera* fma. *attenuata*

SMITH, L. B.

- 6406 *Humiria balsamifera* var. *parvifolia*

- 6694 *Humiria balsamifera* var. *parvifolia*

SPLITGERBER, F. L.

- s.n. *Humiria balsamifera* var. *guianensis*

SPRUCE, R.

- s.n. *Humiria balsamifera* var. *floribunda*

- s.n. *Humiria balsamifera* var. *guianensis*

- s.n. *Sacoglottis guianensis* fma. *glabra*

- s.n. *Schistostemon oblongifolium*

- 164 *Humiria balsamifera* var. *floribunda*

- 181 *Humiria balsamifera* var. *floribunda*

- 763 *Sacoglottis guianensis* fma. *glabra*

- 928 *Humiria balsamifera* var. *floribunda*

- 1009 *Sacoglottis guianensis* fma. *glabra*

- 1499 *Humiria balsamifera* var. *floribunda*
 1714 *Schistostemon macrophyllum*
 1715 *Humiriastrum cuspidatum* var. *cuspidatum*
 1915 *Humiriastrum cuspidatum* var. *cuspidatum*
 1969 *Schistostemon oblongifolium*
 2419 *Schistostemon oblongifolium*
 2424 *Humiriastrum cuspidatum* var. *cuspidatum*
 2443 *Humiriastrum cuspidatum* var. *cuspidatum*
 2454 *Humiria balsamifera* var. *sessilis*
 2457 *Humiria balsamifera* var. *sessilis*
 3073 *Schistostemon oblongifolium*
 3094 *Schistostemon oblongifolium*
 3194 *Schistostemon oblongifolium*
 3409 *Humiria balsamifera* var. *guianensis*
 3419 *Humiria balsamifera* var. *laurina*
 4335 *Humiria balsamifera* var. *parvifolia*
 5963 *Sacoglottis guianensis* fma. *glabra*

STAHEL, G.

- 18 *Sacoglottis guianensis* fma. *guianensis*
 90 *Humiria balsamifera* fma. *attenuata*
 263 *Sacoglottis cydonioides*

STAHEL, G., & GONGGRYP, J. W.

- 3570 *Humiria balsamifera* fma. *balsamifera*

STEYERMARK, J. A.

- 57817 *Humiria balsamifera* var. *laurina*
 57880 *Humiria balsamifera* var. *sessilis*
 58288 *Humiria balsamifera* var. *coriacea*
 59186 *Humiria balsamifera* var. *coriacea*
 59621 *Humiria balsamifera* var. *pilosa*
 60192 *Humiria balsamifera* var. *sessilis*

- 60289 *Humiria balsamifera* var. *pilosa*
 60756 *Sacoglottis guianensis* var. *hispidula*

STEYERMARK, J. A., & WURDACK, J. J.

- 1109 *Humiria balsamifera* var. *coriacea*

TALBOT, P. A.

- 1744 *Sacoglottis gabonensis*

TAMAYO, F.

- 3123 *Vantanea minor*

TATE, G. H. H.

- 50 *Humiria balsamifera* fma. *attenuata*
 142 *Schistostemon oblongifolium*
 209 *Humiria balsamifera* var. *laurina*
 283 *Humiria balsamifera* var. *laurina*
 286 *Humiria balsamifera* var. *laurina*
 330 *Humiria balsamifera* var. *savannarum* (2nd sheet)
 330 *Humiria balsamifera* var. *sessilis* (1st sheet)
 331 *Humiria balsamifera* var. *sessilis*
 733 *Humiria balsamifera* var. *coriacea*
 1113 *Humiria balsamifera* var. *coriacea*

THURN, E. F.

- s.n. *Schistostemon densiflorum*

TRAILL, J. W. H.

- 80 *Humiria balsamifera* var. *guianensis*
 81 *Schistostemon macrophyllum*

TUTIN, T. G.

- 83 *Humiria balsamifera* fma. *attenuata*
 421 *Sacoglottis cydonioides*

ULE, E. H. G.

- 6142 *Humiria balsamifera* var. *guianensis*
 7625 *Humiria balsamifera* fma. *attenuata*

7625 *Humiria balsamifera* var. *floribunda*

8801 *Vantanea minor*

VARESCHI, V., & FOLDATS, E.

4573 *Humiria balsamifera* var. *coriacea*

4673 *Schistostemon auyantepuiense*

5463 *Humiria balsamifera* var. *coriacea*

VERSTEEG, G. M.

265 *Schistostemon dichotomum*

VIGNE, C.

2801 *Sacoglottis gabonensis*

WACHENHEIM, G.

179 *Vantanea parviflora* var. *parviflora*

489 *Vantanea parviflora* var. *parviflora*

WEDDELL, H. A.

526 *Humiria balsamifera* var. *floribunda*

2361 *Humiria balsamifera* var. *floribunda*

WILLIAMS, L.

13868 *Humiria balsamifera* var. *sessilis*

13903 *Humiria balsamifera* var. *guianensis*

15052 *Humiria balsamifera* var. *laurina*

15418 *Humiria balsamifera* var. *laurina*

WILLIAMS, L., & SILVA, N. T.

18201 *Sacoglottis mattogrossensis* fma. *glabra*

WULLSCHLAEGEL, H. R.

1393 *Humiria balsamifera* var. *guianensis*

WURDACK, J. J.

293 *Sacoglottis amazonica*

WURDACK, J. J., & ADDERLY, L. S.

42760 *Humiria wurdackii*

WURDACK, J. J., & MONACHINO, J.

40881 *Humirastrum cuspidatum* var. *cuspidatum*

41149 *Sacoglottis guianensis* var. *hispidula*

41380 *Humiria balsamifera* var. *savannarum*

ZENKER, G.

148 *Sacoglottis gabonensis*

440 *Sacoglottis gabonensis*

1249 *Sacoglottis gabonensis*

1624 *Sacoglottis gabonensis*

1671 *Sacoglottis gabonensis*

1677 *Sacoglottis gabonensis*

1953 *Sacoglottis gabonensis*

2499 *Sacoglottis gabonensis*

2760a *Sacoglottis gabonensis*

4407 *Sacoglottis gabonensis*

Bibliography

- ALLEN, P. H. The rain forests of Golfo Dulce, p. 317. 1956.
- AUBLET, J. B. Histoire des plantes de la Guiane française 1:564, 572, pl. 225 and 229. 1775.
- BAILLON, H. Notes sur les géraniacées et les linacées. *Adansonia* 10:368-371. 1873.
- . Description d'un nouveau genre de la famille des humiriacées. *Adansonia* 2:262-267. 1862.
- . Recherches sur l'organisation et le développement des Ericoidées, Humiriacées. *Adansonia* 1:208-211. 1860-1861.
- . Histoire des plantes, série des Houmiri, 5:51-56, figs. 88-97. Paris, 1874.
- BAKHUIZEN VAN DEN BRINK, R. C. FIL. Humiriaceae in Pulle, Flora of Surinam 3(1):412-421. Amsterdam, 1941.
- BARBOUR, W. F. Note on *Vantanea barbourii* Standley, Tropical Woods 75:7-8. 1943.
- BAUHINO, I. Fructus exoticus cinereus in Historia plantarum universalis nova. Liber III, cap. CX, fig. 1, p. 328. Ebroduni, 1650.
- BENTHAM, G. Contributions towards a flora of South America. Enumeration of plants collected by Mr. Schomburgk, in British Guiana. Humiriaceae, London Journ. Bot. 2:373-375. 1843.
- . Notes on Humiriaceae, Hooker's Journ. Bot. & Kew Gard. Misc. 5:97-104. 1853.
- BENTHAM, G., & HOOKER, J. D. Genera plantarum. 1, Ordo XXXV, Humiriaceae:246-247. 1862.
- BERRY, E. W. Lower Eocene floras of southeastern North America. Prof. Pap. U.S. Geol. Survey 91:255, pl. 54, fig. 6. 1916.
- . Pliocene fossil plants from Eastern Bolivia. Johns Hopkins Univ. Stud. Geology 4:178, pl. VIII, figs. 5-11. 1922.
- . Fossil fruits from the Eastern Andes of Colombia. Bull. Torrey Bot. Cl. 51:64, figs. 20-22. 1924.
- . New tertic species of *Anacardium* and *Vantanea* from Colombia. Pan. Amer. Geol. 42:259, pl. 18. 1924.
- . Tertiary fossil plants from Colombia, South America. Proc. U.S. Nat. Mus. 75, art. 24, pp. 1-12, pls. 1-5. 1929.
- . Fossil fruits in the Ancon sandstone of Ecuador. Journ. Paleontology 3(3):300, figs. 4, 5. 1929.
- . Early Tertiary fruits and seeds from Belen, Peru. Johns Hopkins Univ. Stud. Geology 10:155-157, pl. 1. 1929.
- BULLOCK, A. A. Indicis nominum familiarum angiospermarum prodromus, taxon 7(1):1-35. 1958.
- CASARETTO, G. Novarum stirpium brasiliu decades. I-X in 1 vol. Genuae, 1842-45. Decas IV, 1842.
- CLUSIUS, C. Exoticorum libri decem. Lib. II cap. 19. 1605.
- CROIZAT, L. Manual of phytogeography, or an account of plant-dispersal throughout the world. Humiria:387-388. The Hague, 1952.
- CUATRECASAS, J. New and noteworthy Colombian trees. Tropical Woods 96:37-41. 1950.

- DE CANDOLLE, A. P. *Prodromus systematis naturalis regni vegetabilis* 1:619. 1824.
- DUCKE, A. New forest trees and climbers of the Brazilian Amazon. *Inst. Agr. Norte, Belém-Pará, Boletim Tecnico* 4:Linaceae 13-14. 1945.
- . Plantes nouvelles ou peu connues de la région amazonienne (II^e partie), Humiriaceae. *Arch. Jard. Bot. Rio de Janeiro* 3:175-180, 271, Estampa 10b. 1922; (III^e serie) 4:99. 1925; (IV^e serie) 5:142, pl. 14, figs. 34-41, pl. 17, fig. 42. 1930; (V^e serie) 6:39-40. 1933.
- . Plantes nouvelles ou peu connues de la région amazonienne (VII^e serie), *Arch. Inst. Biol. Veget. Rio de Janeiro* 1:205-207, 1935; (X^e serie) 4:24-31. 1937.
- DUPLESSY, F. S. Des végétaux résineux, tant indigènes qu'exotiques, ou description complète des arbres, arbrisseaux arbustes et plantes qui produisent des résines. A-I:256-259. Paris, 1802.
- ENDLICHER, S. *Genera plantarum*, 1039-1040. Vindobonae, 1840.
- ERDTMAN, E. Pollen morphology and plant taxonomy, angiosperms. Stockholm, 1952.
- GLEASON, H. A. Botanical results of the Tyler-Duida Expedition. *Bull. Torrey Bot. Club* 58:374-375. 1931.
- GMELIN, J. F. *Systema naturae*, Caroli a Linne editio decima tertia. Lipsiae, 1791.
- GUPPY, H. B. Plants, seeds, and currents in the West Indies and Azores. London, 1917.
- HALLIER, H. Beitræge zur Kenntniss der Linaceae. 9 die Humiriaceen. Beihefte Bot. Centralblatt 39, Abt. 2:56-62, 174. 1921.
- HEIMSCH, C. The Gruinales and Terebinthales. Humiriaceae:96-97, pl. 1, figs. 2, 3, 4. *Lilloa* 8. 1942.
- HEMSLEY, W. B. Hooker's icones plantarum, 4 ser. 6:pl. 2521. 1897.
- . Appendix: On the dispersal of plants by oceanic currents and birds. Botany of the *Challenger* Expedition 1:277-304. 1897.
- HILL, A. W. The method of germination of seeds enclosed in a stony endocarp. *Ann. Bot.* 47:873. 1933.
- HOLDRIDGE, L. R., TEESDALE, MYER, LITTLE, HORN & MARRERO. The forests of western and central Ecuador. Forest Service U.S. Dept. Agr. June 1947.
- HUBER, J. Materiales para a flora amazonica VII. Plantae duckeanae austro-guyanenses, pp. 294-436; Linaceae:413; Humiriaceae:413-414. 1909.
- HUTCHINSON, J. The families of flowering plants. 1 Dicotyledons:196-198, fig. 134. London, 1926.
- HUTCHINSON, J., & DALZIEL, J. M. Flora of West Tropical Africa 1:274, fig. 114. London, 1928.
- JOHNSTON, I. The Botany of San Jose Island. Humiriaceae. *Sargentia* 8:52 and 161, pl. 10, fig. 3. 1949.
- JUSSIEU, A. DE. Humiriaceae, in St. Hilaire, Flora Brasil. Merid. 1:88. 1829.
- JUSSIEU, A. L. DE. *Genera plantarum secundum ordines naturales*, pp. 434, 435. 1789.
- KIRCHHEIMER, F. Ueber das Vorkommen einer Gattung der Humiriaceen im Europäischen Tertiär (with bibliography). *Planta* 39:75-90, 2 figs. 1951.
- KUNTH, C. S. Vier Botanische Abhandlungen ueber die Gattung Vantanea, Abhand. Koenigl. Akad. Wiss., pp. 21-24, tab. IID. 1832.
- LAMARCK, M. J. B. Sur une nouvelle espèce de Vantanea. *Journ. Hist. Nat.*, pp. 144-148, pl. 7. Paris, 1792.
- . *Encyclopaedia* 3:139. 1789; 8:334, pl. 471. 1808.
- LE COINTE, P. Amazonia Brasileira (arvores e plantas uteis), 3:475. 1947.

- LEMÉE, A. Dictionnaire descriptive et synonymique des genres de plantes phanérogames 3. 1931; 5. 1934; 6. 1935; 7. 1939.
- . Flore de la Guyane française, 2:167–170. Brest, 1952.
- LINDLEY, J. An introduction to the natural system of botany or a systematic view of the whole vegetable kingdom. Tribe CVII, Humiriaceae: 122–123. London, 1830.
- . The vegetable kingdom or the structure, classification, and the uses of plants. Ed. 3, Humiriaceae: 447–448, fig. 310. London, 1853.
- LITTLE, E. L. A collection of tree specimens from western Ecuador. Caribbean Forester 9(3):247. 1948.
- . New species of trees from western Ecuador. Journ. Washington Acad. Sci. 38:93, fig. 12. 1948.
- MACBRIDE, F. J. Flora of Peru. Linaceae. Field Mus. Publ. Bot. 13(3):628–631. 1949.
- MARTIUS, C. E. P. Nova genera et species plantarum brasiliensium 2:142–148, pl. 199. 1827.
- MAXIMILIAN, PRINZ ZU WIED-NEUWIED. Beitrag zur flora brasiliens. Nova Acta Physico-Medica, Acad. Caesar. Leopold. Carol. Nat. Cur. 12(1):38–41, pl. VII. Bonn, 1824.
- METCALFE, C. R. & CHALK, L. Anatomy of the dicotyledons 1:277–279, figs. 66–M, N. 1950.
- MIQUEL, F. A. G. Stirpes Surinamenses selectae. Lugduni Batavorum, 1850.
- MORRIS, D. A Jamaica drift-fruit. Nature 39:322–323. 1889; 53:64–66. 1895.
- MUELLER, C. Synopsis plantarum phanerogamicarum. Walpers Annales Botanices Systematicae, tomus 4, Humiriaceae, Ordo LIII: 382–385. 1857–58.
- PERBIRA PINTO, G. O óleo de uchí (seu estudo químico). Bol. Tecn. Inst. Agr. Norte 31:187–193. Belém-Pará. 1956.
- PLANCHON, J. E. Sur la famille des Linnées. Hookers London Journ. Bot. 6:588. 1848.
- POST, T. VON, & KUNTZE, O. Lexicon generum phanerogamarum. Stuttgart, 1904.
- PRITZEL, G. A. Iconum botanicorum index locupletissimus. 1866.
- RECORD, S. Random observations on tropical American timbers; Humiriaceae in Central America. Tropical Woods 77:8–9. 1944.
- RECORD, S., & HESS, R. W. Timbers of the New World. New Haven, 1943.
- REICHE, K. Humiriaceae, in Engler & Prantl, Die Natuerlichen Pflanzenfamilien, 3(4):35–37, fig. 32. 1890.
- REID, E. M. Note on some fossil fruits of Tertiary age from Colombia, South Amer. Rev. Geogr. Phys. et Geol. Dynam. 6(3):210–212, pl. 14. 1933.
- RIDLEY, H. N. The dispersal of plants throughout the world. 1930.
- SCHNIZLEIN, A. Abbildungen der Natuerlichen Familien des Gewaechsreiches 3:pl.222, and text (Humiriaceae) without pagination. Bonn, 1843–1870.
- SCHREBER, J. C. D. C. a Linné . . . genera plantarum . . . 8 ed., 1:358. 1789.
- SCOPOLI, I. A. Introductio ad historiam naturalem. Sistens genera lapidum, plantarum et animalium. Pragae, 1777.
- SELLING, O. E. Fossil remains of the genus *Humiria*. Svensk Botanisk Tidskrift 39:258–269, figs. 1–24. 1945.
- SLOANE, H. Catalogus plantarum quae in insula Jamaica sponte . . . p. 214. 1696.
- SPACH, E. Histoire naturelle des végétaux 13. Les Humiriacées. Humiriaceae:297–300. Paris, 1846.

- SPRAGUE, T. A. The correct spelling of certain generic names. Bull. Misc. Inf. Kew 5:241-243. 1929.
- STANDLEY, P. C. A Costa Rican species of *Vantanea*, of the family Humiriaceae. Tropical Woods 75:5-6. 1943.
- ST.-HILAIRE, J. Exposition des familles naturelles, 2:374. 1805.
- . Flora brasiliae meridionalis (Jussieu, Humiriaceae) 2:87-91. 1829.
- URBAN, I. Humiriaceae, in Martius, Flora brasiliensis XII pars 2:425-454, pl. 92-96. 1877.
- . Humiriaceae in P. Taubert, Plantae glaziovianae novae vel minus cognitae. Beiblatt Bot. Jahrb. 15:2-3. 1892.
- . Die Begrenzung der Gattungen in der Familie der Humiriaceae. Sitz.-Ber. Ges. Naturf. Freunde:2-5. Berlin, 1878.
- WEHMER, C. Die Pflanzenstoffe, 2 vols.: 1929, 1931. Ergaenzungsband, 1935.
- WEYLAND, H. Die fossilen Sacoglottis-Früchte und eine neue Art der Gattung, *Sacoglottis germanica* n. sp. Dacheniana, ser. A, 98:163-164. 1938.
- WIESNER, J. Die Rohstoffe des Pflanzenreiches, vierte Auflage, 2 vols. 1927.
- WILLDENOW, C. L. Species plantarum (Caroli a Linné) 2:1172. 1800.
- WILLIAMS, R. O. Flora of Trinidad and Tobago, Humiriaceae, vol. 1 (part 2):150-151. 1929.
- WINKLER, H. Unterfam. IV, Humirioideae, in Engler & Prantl, Die Natuerlichen Pflanzenfamilien, zweite Auflage. Band 19a, 106, 126-129, figs. 58, 59. 1931.

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U N I T E D S T A T E S N A T I O N A L M U S E U M

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3. ORIGINS OF THE FLORA OF SOUTHERN BRAZIL

4. A SYNOPSIS OF THE AMERICAN VELLOZIACEAE

By LYMAN B. SMITH



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PART 3

ORIGINS OF THE FLORA OF SOUTHERN BRAZIL

LYMAN B. SMITH

Ever since the first land plants evolved, the face of the earth has been changing constantly, so that we may safely assume that the flora of any given region today has arrived from somewhere else. In the case of land recently risen out of the sea, it is relatively easy to see whence its flora came, but in the case of a great center of distribution like the Amazon Basin it is difficult if not impossible to reconstruct its past.

Southern Brazil, which is to say the states of São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, is an intermediate case. The area is not recently exposed except for a narrow coastal fringe, but on the other hand, most of its plant families have their greatest development elsewhere. Thus there are some fairly obvious lines of migration (fig. 1), and the continuity of some ranges and the discontinuity or disjunction of others indicate that these migrations have taken place at different times. The flora of the coastal rain forest is a direct continuation and attenuation of that centering on Rio de Janeiro, while the flora of the campos or rolling prairies of the planalto has a similarly direct origin from the central states of Minas Gerais and Goiás. There is another continuous migration pattern from northern Argentina and Paraguay eastward and a considerable amount from the Andes. We have a few wide ranging maritime species extending from the north into the area, but from due south there is relatively little evidence of immigration, possibly because this area may not have emerged from the sea until a later date.

The discontinuous ranges follow much the same migration routes as the continuous ones from the north, but these are suspect as being due to gaps in collecting. Of those based on fairly firm evidence the most important by far are the Andean, with only a few species each for the Austral, coastal plain, and African.

It may seem presumptuous and reckless to discuss ranges at all on the basis of such meager evidence as we now have, and probably we

still need several hundred years of collecting and classifying before the flora of Brazil is really well known. However, there are certain broad physiographic regions that are readily recognizable even if they do blend at the boundaries, and while collecting and classifying we become aware of phytogeographic patterns that correlate with them, like a picture slowly coming into focus. Furthermore we cannot afford to wait indefinitely because the rapid advance of agriculture is eliminating the native flora over much of Brazil.

Maritime Zone

There is always a seacoast and the highly specialized halophytic flora closely follows its extremely narrow and infinitely long zone. For thousands of miles one can pick a stretch of Brazilian coast at random and know that he can find *Ipomoea pes-caprae* (pl. 1) and *Remirea maritima* (fig. 2) on the sand just above high-tide mark or *Rhizophora mangle* (pls. 1, 2) at the seaward end of an estuary. Higher up in the restinga or scrub forest zone or on saltmarsh will be *Hibiscus tiliaceus*. If we had complete records of these species their ranges would form an almost continuous line on the map. This assumption is one of the safest that we will make because maritime conditions are much the same the world over.

However, the maritime flora of southern Brazil has one unusual feature when compared to those familiar in the Northern Hemisphere. So far as present evidence shows, its wide ranging species are all of tropical derivation and none of circumpolar. The list of such strictly or predominantly maritime species would include:

- Sporobolus virginicus* (Gramineae)
- Stenotaphrum secundatum*
- Remirea maritima* (Cyperaceae)
- Salicornia virginica* (Chenopodiaceae)
- Canavalia rosea* (Leguminosae)
- Hibiscus tiliaceus* (Malvaceae)
- Rhizophora mangle* (Rhizophoraceae)
- Conocarpus erecta* (Combretaceae)
- Laguncularia racemosa*
- Hydrocotyle bonariensis* (Umbelliferae)
- Ipomoea pes-caprae* (Convolvulaceae)
- Scaevola plumieri* (Goodeniaceae)

Some of the above like *Sporobolus virginicus* and *Stenotaphrum secundatum* (fig. 3) although predominantly maritime also occur inland. Species like *Rhizophora mangle* on the Ilha de Santa Catarina, reach their limits in southern Brazil, while others extend beyond, but apparently none are found south of the province of Buenos Aires.

There are a number of subtropical species that are common in the

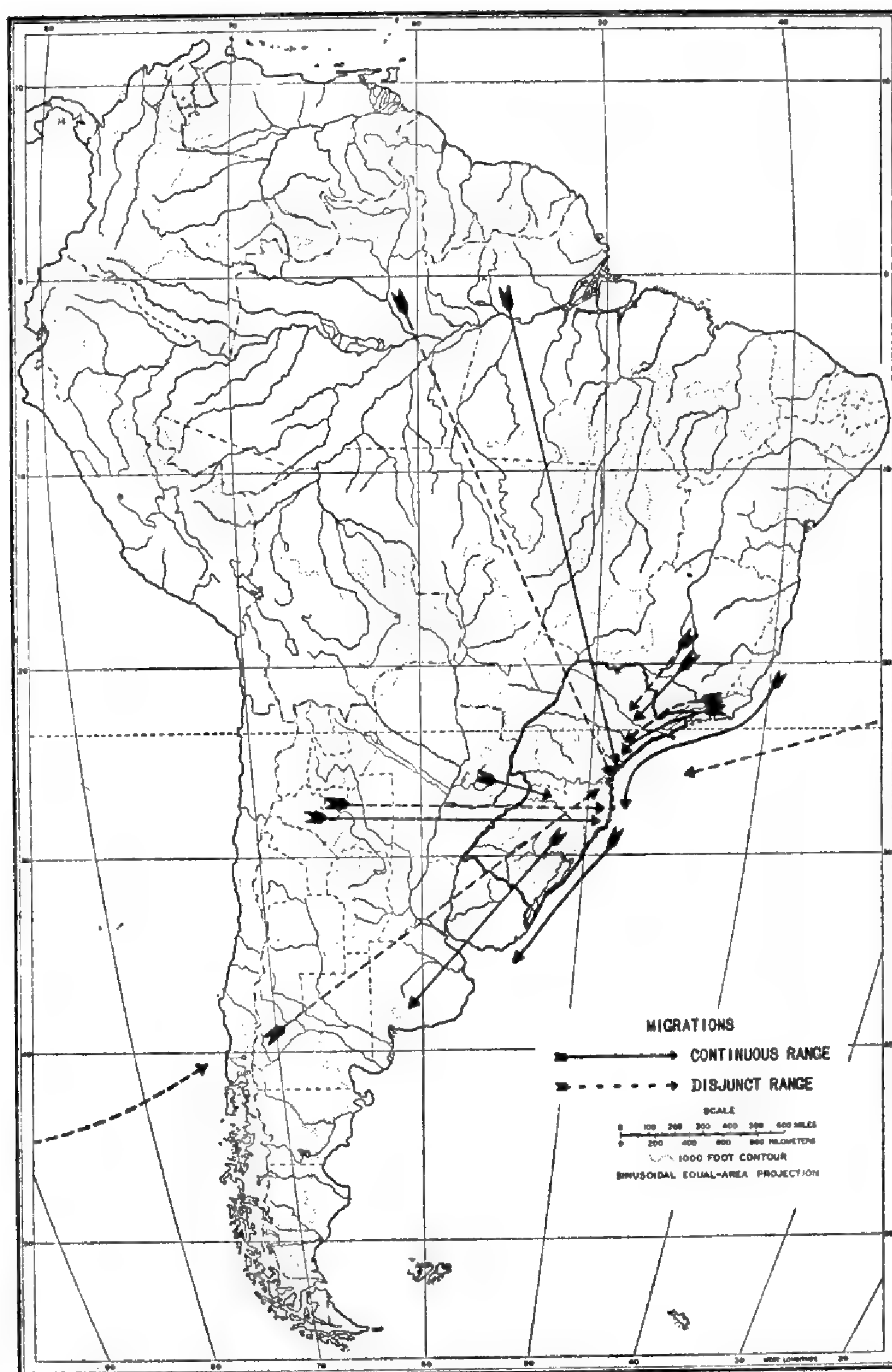
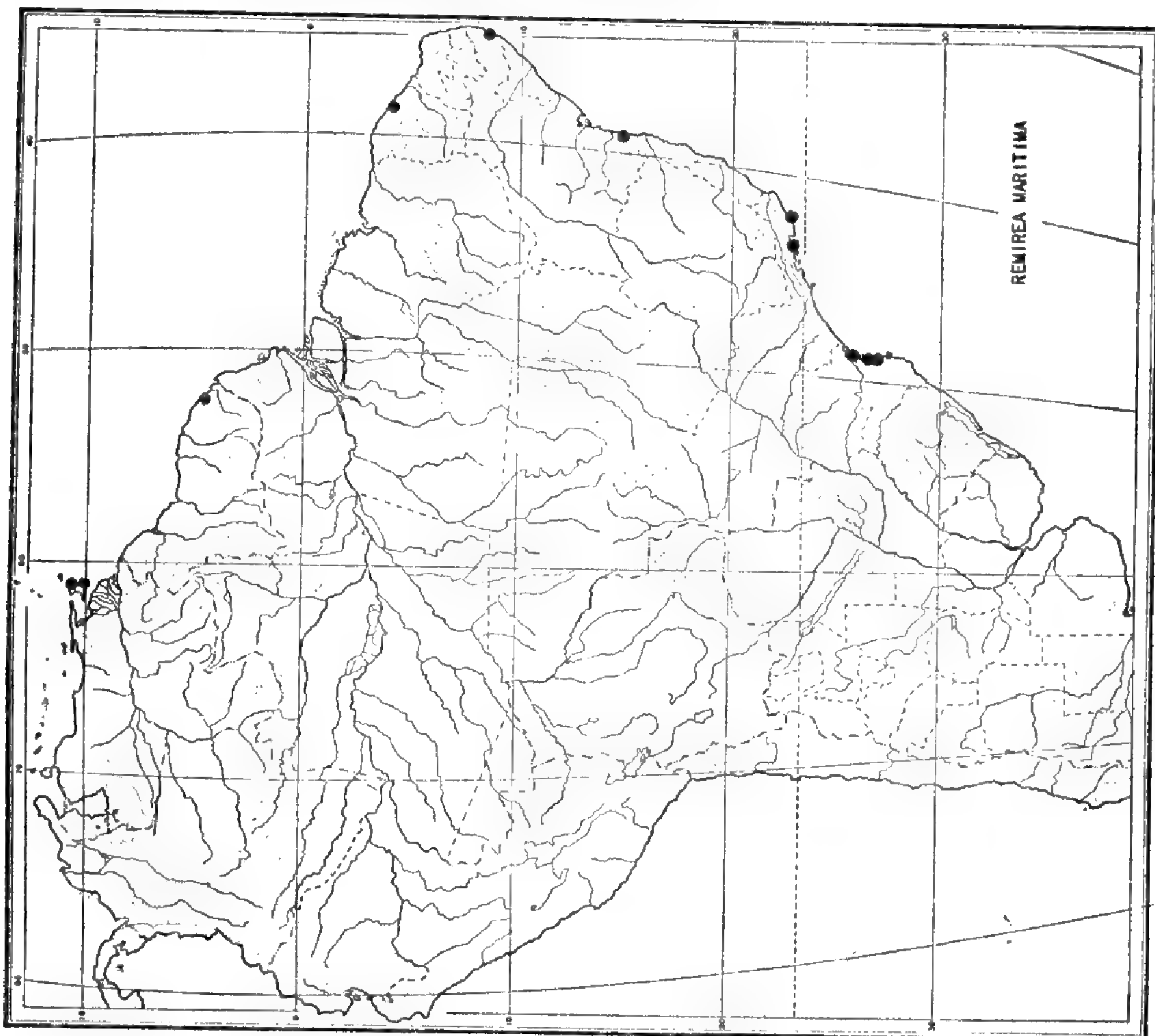
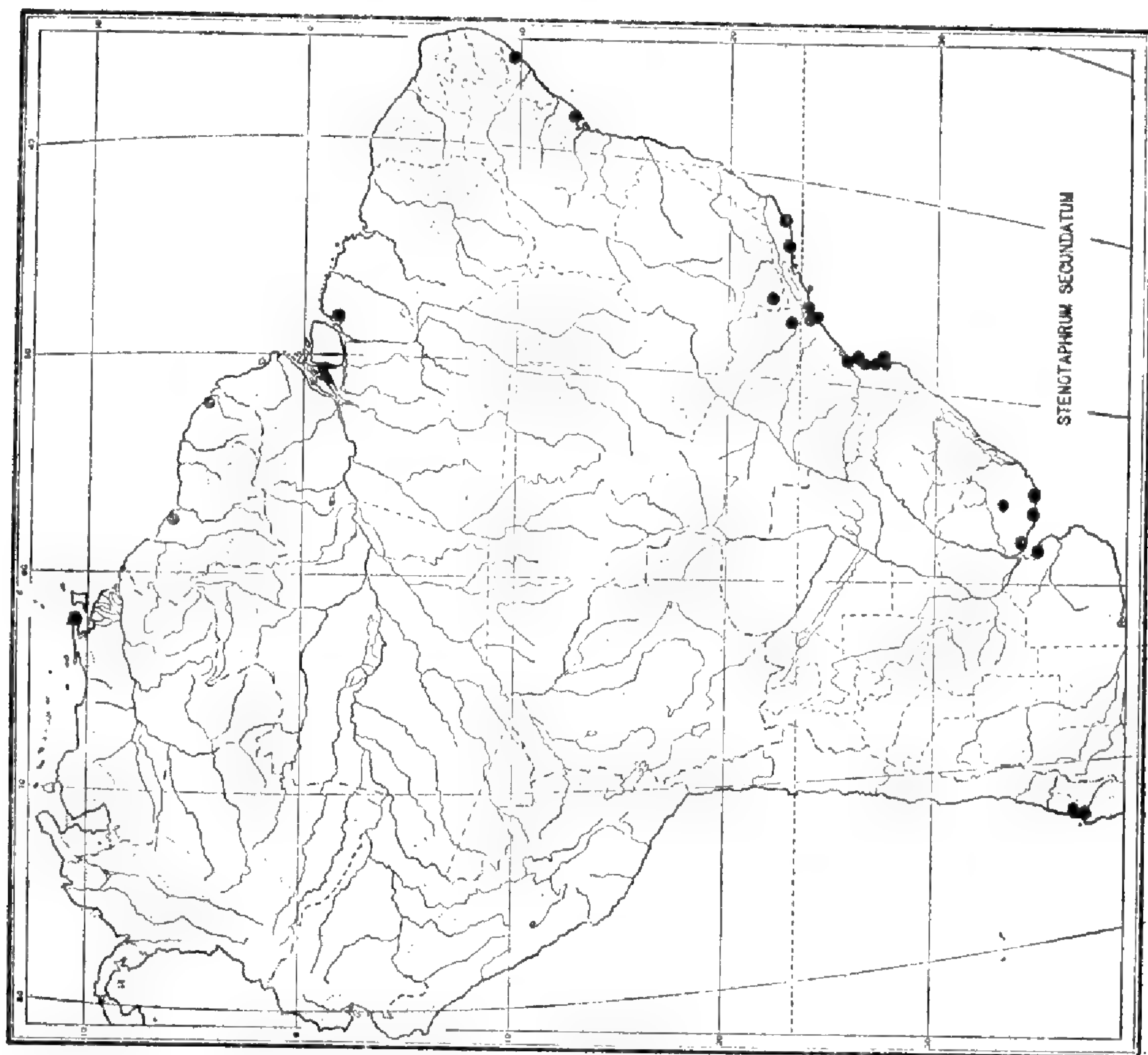


FIGURE 1.—Different types of migration into southern Brazil.

maritime zone from southern Brazil to Uruguay and the province of Buenos Aires. Among them may be noted:

- Triglochin striata* (Scheuchzeriaceae)
- Androtrichum trigynum* (Cyperaceae)
- Chenopodium retusum* (Chenopodiaceae)
- Alternanthera maritima* (Amaranthaceae)
- Acicarpa spathulata* (Calyceraceae)

FIGURE 2.—Maritime migration: *Remirea maritima*.FIGURE 3.—Maritime migration: *Stenotaphrum secundatum*.

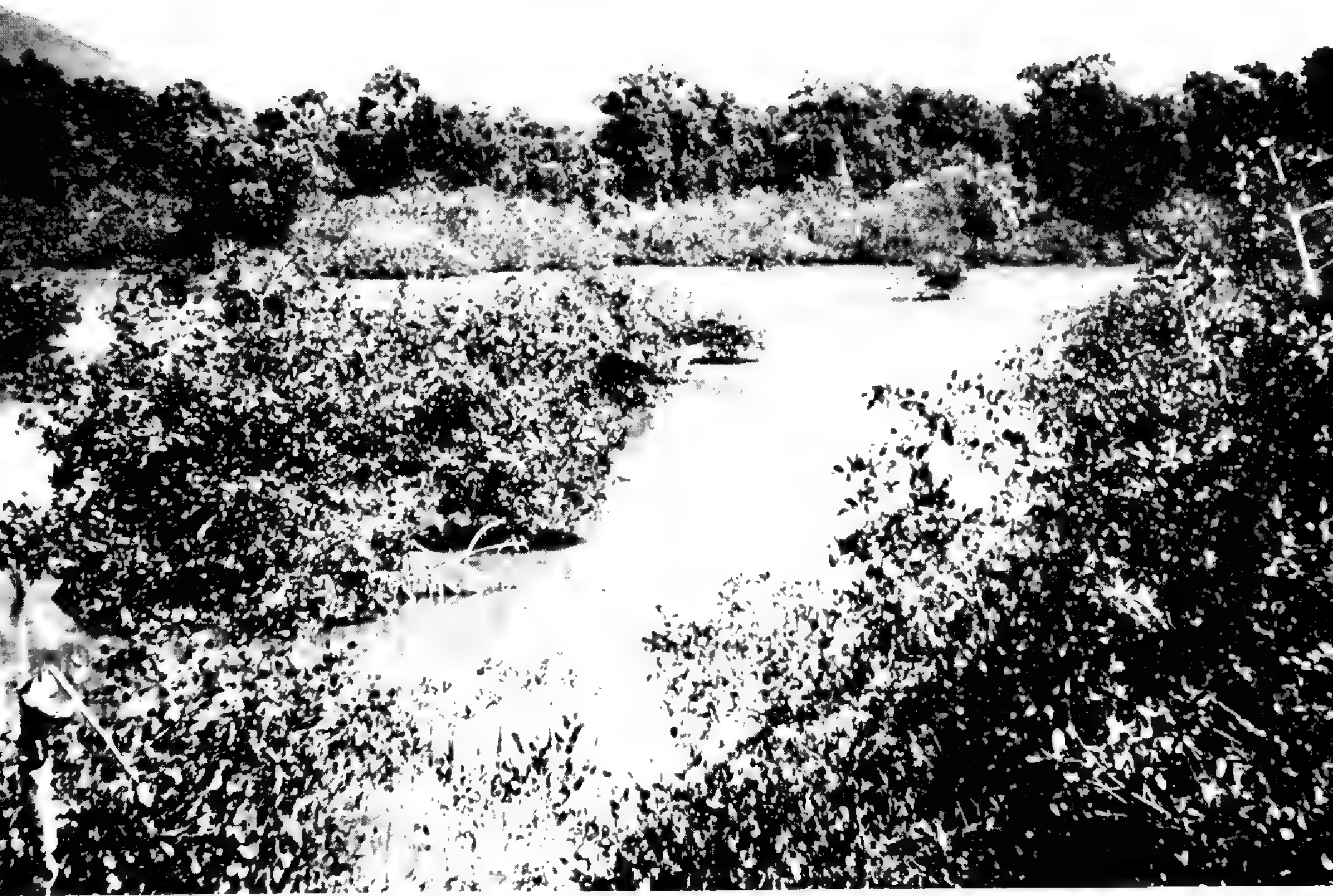


PLATE 1. Santa Catarina. *Rhizophora mangle* in estuary, Florianópolis. Bottom:
Sea beach at Itaipã; prostrate vines of *Ipomoea pes-caprae* in foreground.



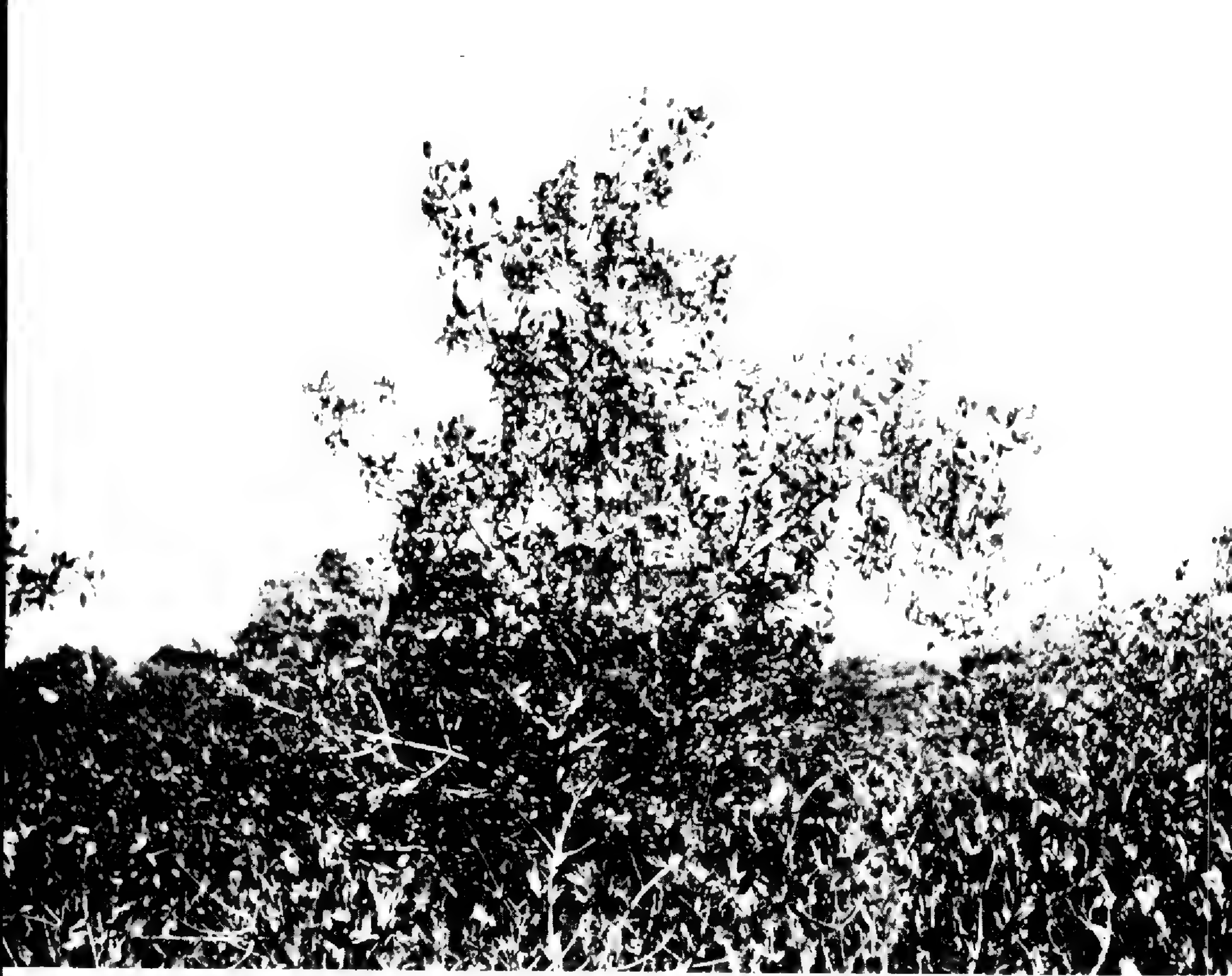


PLATE 2. *Rhizophora mangle*, showing pendulous viviparous fruit. Bottom: Coastal rain forest, from top of the Spitzkoppe, Blauwoud, Santa Catarina.





PLATE 3. Pedro de Gueva, Rio de Janeiro, Brazil. The photograph shows the coastal rain forest. Below the plateau, the forest is dense and lush. The flowers of *Barringtonia speciosa* are visible in the foreground.





PLATE 4. Santa Catarina. Gallery forest along streams in campo of planalto, near Lajes.
Bottom: *Araucaria* forest.



At first glance one might suppose that some of these arrived from the south, but in each case checking reveals that more likely the migration was in the opposite direction or from the west across northern Argentina. Whether southern Argentina was submerged in recent times or not, its present climate appears to be too arid to allow any trace of southern connections below the province of Buenos Aires.

The maritime zone is unlike any of those that follow in that it includes no disjunct ranges. This situation is no more than might be expected from the continuous and constant ecological conditions that it provides.

Coastal Rain Forest

The coastal rain forest (pl. 2) extends some 2000 miles or 3200 kilometers from extreme northern Rio Grande do Sul to the Herval and Tapes Ranges in Rio Grande do Norte. Thus it is about the same length as the Amazonian rain forest though only a fraction of the width. A flight from Trinidad to Rio de Janeiro takes several hours to cross the Amazonian forest but only minutes to cross the coastal. In general the western boundary of the coastal forest is the height of land from which the sea is visible from many points. Only in Santa Catarina does this zone extend inland to a depth of about 100 miles or 160 kilometers.

In relation to its area the coastal rain forest must be fully as rich in species as the Amazonian but the representation by families differs greatly. Some families like the Vochysiaceae (Stafleu, 1948) are obviously remnants of much larger ones of the Amazonian forest, while others like the Bromeliaceae (Smith, 1934) have formed a new center in the coastal forest and evolved many new species and genera. The center of speciation of the coastal rain forest is very close to Rio de Janeiro, now the state of Guanabara. From there the flora deteriorates north and south, so that in the area we are considering the species decrease regularly from São Paulo to northern Rio Grande do Sul.

For example the species of the genus *Vriesea* (Smith, 1955) in the Bromeliaceae are distributed from north to south as follows:

	<i>Species</i>
Espirito Santo	31
Rio de Janeiro and Guanabara (former Federal District) . .	54
São Paulo	31
Paraná	26
Santa Catarina	28
Rio Grande do Sul	7

The areas of rain forest are not all commensurate, but the comparison between the first three is fairly close on this score. Paraná has much less rain forest and Santa Catarina with its westward bulge much

more, and Rio Grande do Sul only a remnant. If these scores were to be weighted by areas there would be a fairly regular gradation from Rio de Janeiro southward. On the other hand, Rio de Janeiro enjoys the advantage of the greatest amount of collecting, so if this factor could be weighted also, Rio would not stand quite so high above the others.

More graphic pictures of the situation, though unfortunately for a smaller area, are given by Reitz (1953, 1957) for the Palmae (fig. 4) and Araceae (fig. 5) of Santa Catarina. Both show an overlapping pattern of southern species limits like wave marks on a strand or tiles on a roof, presumably due to the differential tolerance of the various species to minimum temperatures. The point was made dramatically when the boom of southward expansion of coffee cultivation was stopped by a severe winter with unexpected frosts.

Reitz's map of the Araceae shows another feature of distribution, the evolution or isolation of local species in a wide ranging genus, *Anthurium*, thus bringing in the element of time in migrations. The other species of *Anthurium* have expanded southward into Santa Catarina without essential change, while the ancestral stock of *A. lacerdae* and *A. pilonense* has not only migrated over the same route but developed new species as well. Whether their present restricted range is due to newness or shrinking from a wider area, it still indicates an earlier arrival for the parent stock than the species that are

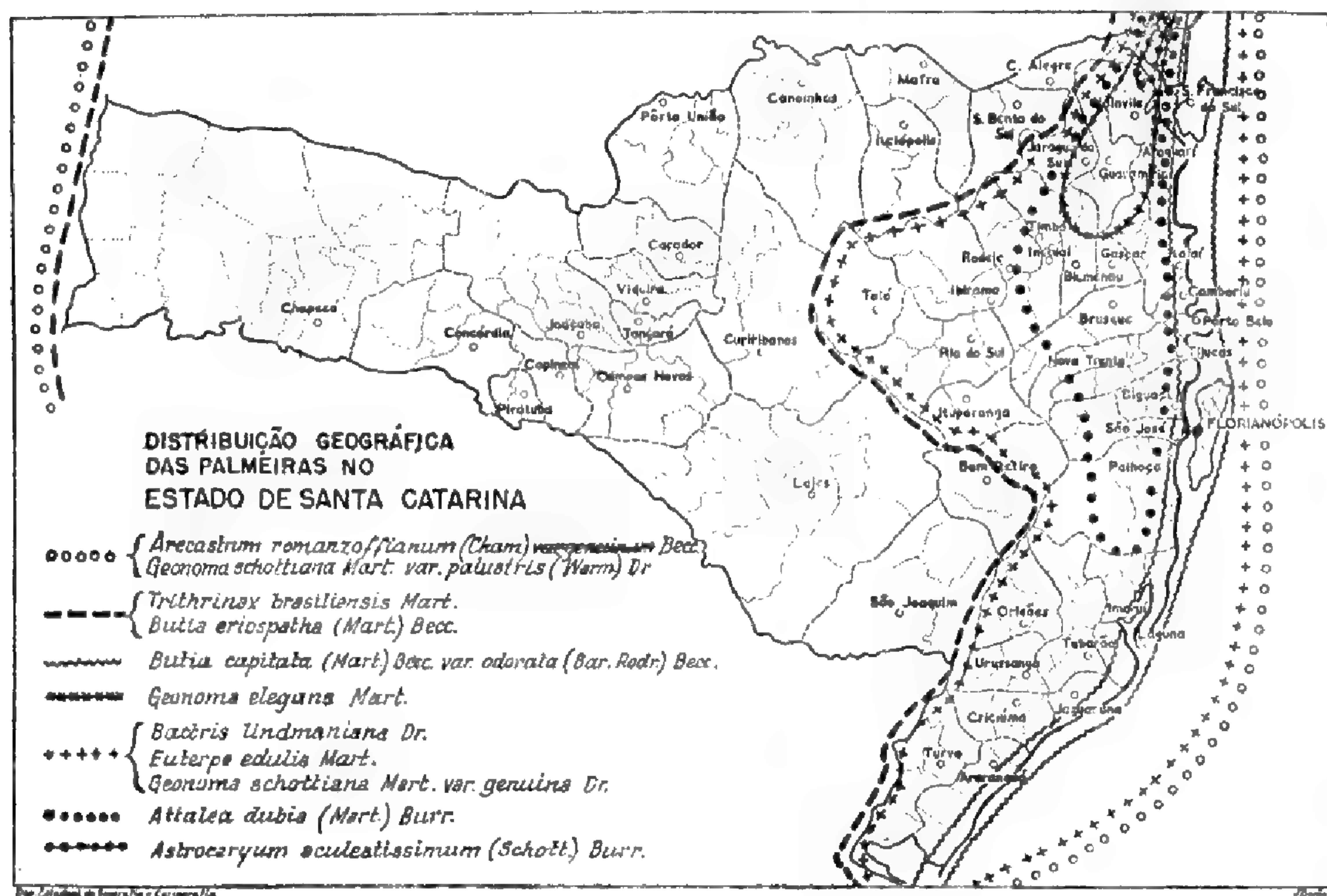


FIGURE 4.—Rain forest migration: Palmae. After R. Reitz 1953.

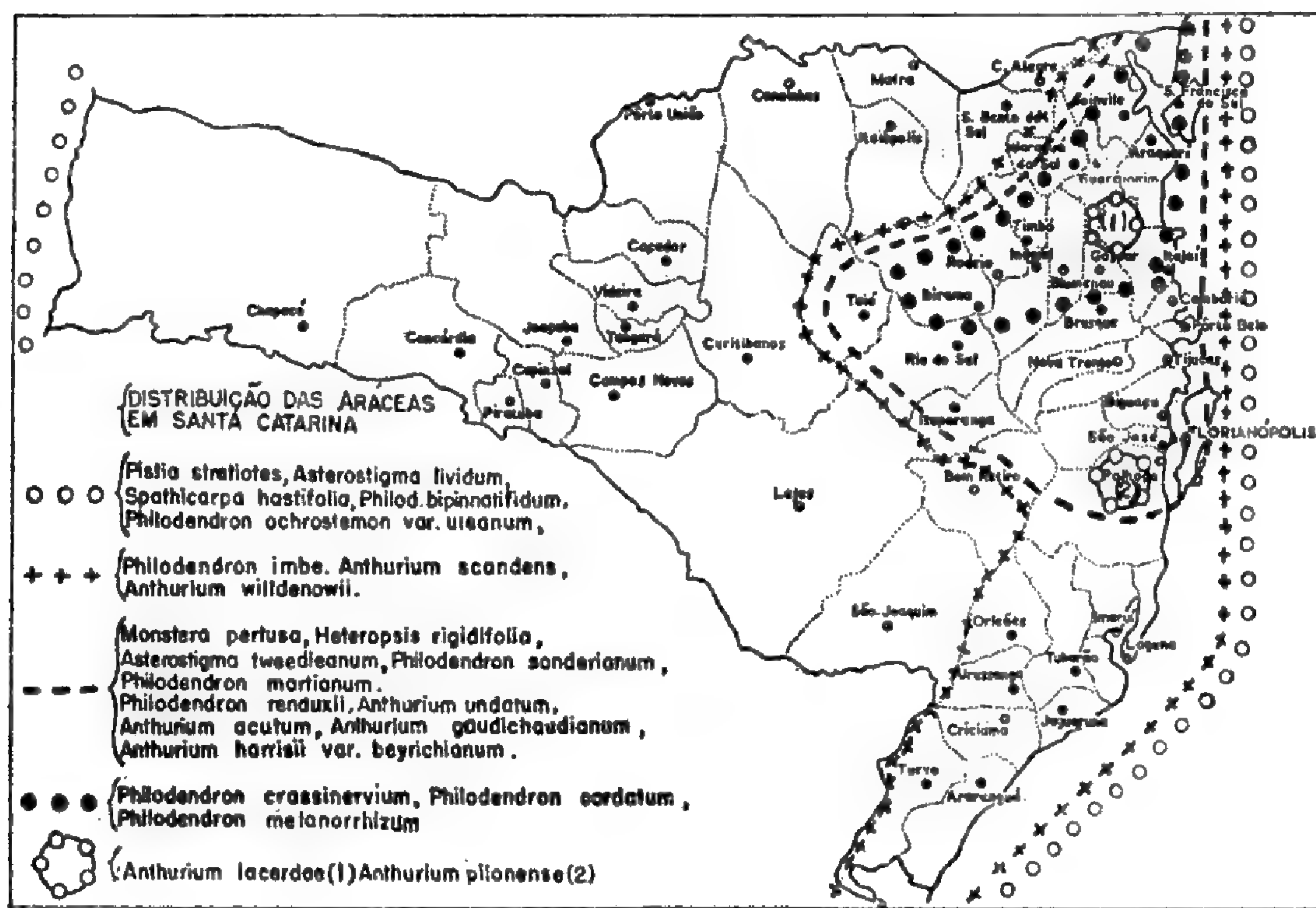


FIGURE 5.—Rain forest migration: Araceae. After R. Reitz 1957.

unchanged. Admittedly there is a possibility that in some cases species have evolved at different speeds, otherwise we should not have any primitive forms of life left in the world. However, within the same genus it would seem less likely for such a difference to be large. The same comparison may be found between genera in different families, where *Vantanea compacta* (fig. 6) is the sole representative of the Humiriaceae (Cuatrecasas, 1961) from Rio de Janeiro to Santa Catarina, while *Quesnelia* (fig. 7) of the Bromeliaceae (Smith, 1955) is represented by several species in Rio de Janeiro and Guanabara, a different set in São Paulo, and still another in Paraná and Santa Catarina. The probability is that *Vantanea* arrived in the rain forest of Santa Catarina ahead of *Quesnelia*, the year to year change of position in migration being more perceptible than the change of form in evolution.

The rain forest of southern Brazil also shows evidence of migration from the Amazonian rain forest (fig. 1), though of course to a much lesser degree than from the much closer center of Rio de Janeiro. The smallness of the Amazonian element is easy to understand when one considers the extensive barrier interposed by the high dry planalto area that lies between the two rain forests for a minimum distance of over 700 miles or 1100 kilometers. For many genera and even some families this climatic barrier is as effective as an ocean. Others, however, have found a bridge across through the network of gallery

forests (pl. 4) that break up the area. The extent and effectiveness of this planalto barrier has fluctuated in the past and is still visibly fluctuating now. As has long been pointed out, new young tree growth invades the campo or prairie of the planalto as the climate grows moister or dies back as it grows drier. This is comparable to the constantly shifting division between long grass and short grass prairie in central United States and Canada.

The different patterns of migration from the Amazonian rain forest would indicate that there have been major fluctuations in the climate so that the barrier of the planalto has been bridged at different times for different groups of plants. Beginning with the migrations that appear most recent because the species extend across northern and central South America without any noticeable change or at most with forms that show no geographic correlation, we have (figs. 8-10):

Protium heptaphyllum (Burseraceae—fig. 8, Swart, 1942)

Tapirira guianensis (Anacardiaceae—fig. 9)

Amaioua guianensis (Rubiaceae—fig. 10, Smith & Downs, 1956)

These trees must have migrated by gallery forest or there may have been continuous broad rain forest between the Amazon and the east coast under more favorable conditions.

Other species combine Amazonian and Andean distribution and appear to have spread southward through thinner forest at higher elevations. Such are (figs. 11-13):

Chlorophora tinctoria (Moraceae—fig. 11)

Casearia silvestris (Flacourtiaceae—fig. 12)

Psychotria carthagenensis (Rubiaceae—fig. 13, Bacigalupo, 1952)

On present evidence they have flanked the planalto rather than crossed it, but further collecting in the interior could change this picture considerably.

There are also certain weedy species that are not truly Amazonian but show much the same overall distribution, not because they are characteristic of the forest but because they immediately take advantage of any break in it, however small. Such are (figs. 14-16):

Axonopus compressus (Gramineae—fig. 14, Black, ined.)

Xyris caroliniana (Xyridaceae—fig. 15, Smith & Downs, ined.)

Polygonum punctatum (Polygonaceae—fig. 16)

At the other extremity of distributional types is the case of the genus *Vochysia* (fig. 17). Here nearly the same area has been covered, but the migration has been so slow that there has been time for the evolution of a completely new set of species on the planalto and almost another in the coastal rain forest. There is also the disjunct of *Quiina* (fig. 18, Pires, ined.) with one species, *Q. glaziovii*, on the coast and the remainder confined to the Amazon basin. This may indicate a still older migration because of the absence of planalto species, although there is always the possibility of others turning up there.

The migration appears to have taken place at different points all across the planalto judging by the occurrence of some species over nearly the entire length of the coastal rain forest. A very few like *Chlorophora tinctoria* (fig. 11), *Casearia silvestris* (fig. 12), and *Psychotria carthagenensis* (fig. 13) have even connected with the Rio Paraguay Basin and entered southern Brazil across the top of Rio Grande do Sul, meeting the final segment of the coastal rain forest in the northeast corner of the state. However, the Amazonian element is minor, the Paraguayan Basin having developed a flora of its own to an even greater extent than has the coastal rain forest.

Paraguayan Rain Forest

The rain forest of the Rio Paraguay Basin is not a continuous area comparable to the Amazonian or the coastal rain forests but a collection of gallery forests that are so broad that they merge when large rivers lie close together as in the Misiones Territory of Argentina. A comparison of Richards's description of typical rain forest (Tropical Rain Forest, pp. 2-7) and Hauman's of that in Misiones (La Vegetacion de la Argentina, pp. 14-41) shows agreement in all details, yet Richards in his figure 2 follows A. C. Smith and Johnston (Verdoorn, Plants and Plant Science in Latin America, pp. 12, 13) in ignoring this area on his map. Hoehne (Ind. Pl. Com. Rondon, p. 12) and Rambo (Sellowia, No. 7, p. 185) both emphasize the gallery character of this rain forest and their view is much broader than Hauman's, so that Richards after all would seem justified in not including this area had he not included similar fragments in northern South America.

Be that as it may, the southern part of the Paraguayan forest extends over eastern Paraguay, Misiones, and the extreme western parts of Paraná, Santa Catarina, and Rio Grande do Sul, and has developed a very distinctive flora. It has invaded southern Brazil up the Rio Uruguay and its tributaries, and its migration shows the same overlapping pattern of distribution as that of the coastal rain forest but with an eastward instead of a southward direction. In Santa Catarina where it is known as "mato branco" the forest is quite obviously expanding up the river valleys and invading the Araucaria and campo zones (personal field observation and Klein, 1960). Rambo notes the same movement in Rio Grande do Sul. Of the four hundred species listed for the upper Rio Uruguay by Rambo (1956a, pp. 191-207) special mention might be made of the following to illustrate the type of ranges in the Paraguayan forest flora (figs. 19-26):

Pseudoplantago friesii (Amaranthaceae—fig. 19, Smith & Downs, 1960)

Balfourodendron riedelianum (Rutaceae—fig. 20, Cowan, 1960)

Holocalyx balansae (Leguminosae—fig. 21, Burkart, 1943)

Bernardia pulchella (Euphorbiaceae—fig. 22, Smith & Downs, 1959)

Euphorbia sciadophila (Euphorbiaceae—fig. 23)

Diatenopteryx sorbifolia (Sapindaceae—fig. 24, Radlkofer, 1931–34)

Patagonula americana (Boraginaceae—fig. 25)

Dunalia breviflora (Solanaceae—fig. 26, Sleumer, 1950)

Some species have rather restricted ranges like *Pseudoplantago friesii* and *Holocalyx balansae*, while others such as *Bernardia pulchella* and *Dunalia breviflora* have crossed the planalto and the divide and entered the coastal rain forest. It has been claimed that new or isolated species do not occur in the Paraguayan forests of southern Brazil, which would indicate a recent migration. Certainly they are not so evident as in the coastal rain forest. On the other hand, such monotypic endemics as *Pseudoplantago* (fig. 19), *Aphaerema* (Flacourtiaceae), and *Schenckia* (Rubiaceae), would argue a rather distant origin for the Paraguayan forest flora as a whole.

Northern Campo Flora

The campo or prairie flora of southern Brazil derives in part from the central Brazilian highland or planalto and in part from the Andes. It is a crazy quilt cut by a fine dendritic pattern of angiosperm gallery forest in much of São Paulo and Rio Grande do Sul and occurring only as isolated openings in the Araucaria formation of Paraná, Santa Catarina, and northern Rio Grande do Sul. It is considered by some to be the oldest of the large formations and the lack of a well defined pattern of distribution would support the idea. Several families and many genera center in Minas Gerais on the planalto, but it is even more difficult than in the Amazonian flora to find species with a continuous distribution into southern Brazil.

The Velloziaceae (fig. 27), one of the most characteristic families of Minas Gerais, well illustrates this situation. The plants grow on dry barren slopes and crests and the species in most cases have small ranges. The few that reach southern Brazil are isolated species known from a single locality each. Incidentally this family also illustrates a fallacy of some plant geographers. Its world range has been shown as a line enclosing the whole Amazon basin, while its true occurrence there is limited to a few bare peaks near the edge of it. Similarly the points indicated for Velloziaceae in the area of the coastal rain forest all represent bare granite peaks rising above the forest (pl. 3).

Perhaps *Dyckia* (fig. 28) in the Bromeliaceae is a better example because it ranges over the planalto of all southern Brazil and beyond, though it does include more species on the coast and in open spots in the coastal rain forest. Again the species are mostly narrow endemics. There are 28 species in Minas Gerais against only 2 in Rio de Janeiro and Guanabara showing that it is truly a genus of the planalto, and

the numbers hold up well southward with 7 in São Paulo, 8 each in Paraná and Santa Catarina, and 9 in Rio Grande do Sul.

The Eriocaulaceae are undoubtedly the most extreme case of high concentration in Minas Gerais rapidly dwindling out in southern Brazil as the distribution of the species of *Paepalanthus* illustrates (from Moldenke, 1959 a-b, 1960):

	<i>Species</i>
Minas Gerais	660
Rio de Janeiro and Guanabara	21
São Paulo	27
Paraná	9
Santa Catarina	8
Rio Grande do Sul	5
Paraguay	2
Argentina	0
Uruguay	0

It has been difficult to find single species to illustrate the full sweep from the central planalto south, which is probably another indication that the flora is old and that its genera have had time to break up by evolving new species to fit local conditions. Either the ranges are too limited to give a good illustration or they spread out into the coastal zone taking advantage of open areas and thus are not wholly typical of the planalto. However, the following give some idea of the situation (figs. 29-33):

Esterhazyia splendida (fig. 29—partly coastal) (Barroso, 1952)

Baccharis anomala (fig. 30—partly coastal)

Baccharis megapotamica (fig. 31—not known to be coastal)

Vernonia nitidula (fig. 32—partly coastal)

Vernonia platensis (fig. 33—not known to be coastal)

Some species like *Lobelia camporum* are found throughout the campo of southern Brazil up to the highest points but are indifferent to altitude and occur also at low levels along the coast. Even such species of general distribution in the area are disjuncts in a sense because the campo itself is disjunct and does not provide the means of a continuous range.

Andean Flora

The genera that have invaded southern Brazil from the Andes show the greatest diversity in distribution of all that we have studied so far, indicating the longest time elapsed during the migrations from first to last. Some genera include single species that bridge the gap and go far beyond, while others are widely disjunct with few, localized, and distinct species on either side. The first represent extremely recent migrations and the second ancient ones and there are many intermediate cases.

The recent type of migration is shown by *Tillandsia usneoides* (fig. 34) of the subgenus *Diaphoranthema*. Its range is so large that it is thought of as neotropical. Yet its kindred are all represented and in some cases confined to a small area in northwestern Argentina and vicinity (Smith 1934, 1935). Further testimony of its Andean origin and preference for cool climate is shown by its avoidance of the Amazon basin and its extension in the United States as far north as Virginia, the extreme point in the Bromeliaceae by over 500 miles or 900 kilometers. Its recent evolution is shown by its highly specialized structure, with the inflorescence reduced to a single flower and the leaves taking over the functions of the lost roots. Everything points to *Tillandsia usneoides* having been the latest invader of southern Brazil from the Andes.

However, most genera of Andean origin do not include single species extending all across South America and have a maximum distribution in the east from slightly north of Rio de Janeiro to Uruguay. Almost all of these have the greater part of their eastern range in the four southern Brazilian states and many do not extend beyond. Also in the larger examples of this pattern there is a link across northern Argentina to the area of distribution in the Andes. The species of southern Brazil are plants of cool moist climates and have their center of speciation on the crests of the divide and from there extend westward on the planalto mingling and competing with the flora of the northern campo zone. The species connecting across northern Argentina are necessarily more tolerant of heat and aridity than those on either side of them. The ranges of the Andean genera have been pinched in the middle by the southward push of Amazonian heat and the northward push of Patagonian aridity (fig. 35). In many cases the link has been completely broken. This situation makes interesting comparison with North American disjunctions between east and west where glaciation has been used as an explanation. The most recent glaciation in South America preceded flowering plants, so that climate alone accounts for not only the occurrence of the disjunction but for its continuance also.

One of the best examples we know of a wide ranging Andean element in southern Brazil is the genus *Hypericum* (fig. 36). It has numerous species endemic to the Andes and 25 found only in eastern South America (Smith, 1958b). *Hypericum connatum* by a strange coincidence is the link across, its name referring not to this but to its perfoliate leaves. In addition to what is indicated on the map, there is *H. mutilum* of North America occurring on both sides of South America apparently from pre-Columbian times, *H. perforatum* recently naturalized from Europe, and *H. gentianoides*, a natural disjunct with North America.

The genus *Berberis* (fig. 37—Schneider, 1904–05) has an overall appearance in South America much like *Hypericum*, but has a single disjunct species, *B. montana*, occurring in central Chile and on Campo dos Padres, the highest peak in Santa Catarina. It is thus intermediate between *Hypericum* and the genera that are completely disjunct.

Herreria (fig. 38) is unusual in having more species in the east than in the west (Smith, 1958a) and unlike *Hypericum* and *Berberis* does not occur outside South America. It still has a link across northern Argentina. *Viviania* (fig. 39), however, has lost all connection and has no species common to both areas (Knuth, 1912). *Crinodendron* (fig. 40) is similar but its representation in southern Brazil is limited to *C. brasiliense* (Reitz & Smith, 1958), endemic to the peak of Campo dos Padres.

Araucaria (fig. 41) is represented by *A. angustifolia* in southern Brazil (pl. 4) and *A. araucana* in the southern Andes on the Argentine-Chilean boundary, and by a number of species in Australia and the southwestern Pacific region. The disjunction is the longest we have met of this type, some 1100 miles or 1800 kilometers, and at the same time the most certain. Herbs or low shrubs might be overlooked in some sheltered spot in the interval, but there is no chance of hiding the stately pinheiro. It still shows movement as its heliophile progeny slowly invade the campo, but on the other side it is losing at a much faster rate to the inroads of the Paraguayan forest and to man (Klein, 1960).

Cordyline (Baker, 1875) of the Liliaceae has a range much like that of *Araucaria* except that there is no Andean species known to link *C. dracaenoides* (fig. 42) of southern Brazil with the rest of the genus on the other side of the Pacific. It might equally well be classed with our overseas disjuncts except for this similarity.

Overseas Disjuncts

Under the title of overseas disjuncts we have a miscellany of odds and ends, some of which are probably pre-Columbian arrivals in southern Brazil and others that are not, but are obvious weedy newcomers. Sometimes it is difficult to decide which. *Arenaria groenlandica* on a single peak in Santa Catarina (Smith & Downs, 1960b) and known elsewhere from Georgia to Greenland in North America hardly seems likely to be a weed. *Hypericum gentianoides* of Rio Grande do Sul, Paraguay, and eastern United States (Smith, 1958b) might possibly be a recent introduction, but Rambo who found it in Brazil, thinks it unlikely because of the habitat. *Proserpinaca palustris* (Reitz, 1954) of Santa Catarina and Rio Grande do Sul is indistinguishable from the North American plant. The three taken together and compared with a more nearly continuous range such as that of *Utricularia subulata* make a fairly consistent pattern.

Links with Africa, whether specific like *Xyris anceps* and *X. capensis* or generic like *Pitcairnia* and *Rhipsalis*, are indirect, with the South American center lying to the north of the area we are considering. The European links, so far as I have been able to ascertain, are all recent weedy introductions. Rambo has covered much of the details of this flora (1960) and its origin is too obvious to need discussion here. If his list is anywhere near complete it would indicate that southern Brazil is not so badly overrun with weeds as are equivalent latitudes in North America.

Acknowledgments

The present paper is an enlargement of one presented at the ninth International Botanical Congress at Montreal in 1959. Unless otherwise noted the range maps have been compiled from specimens in the United States National Herbarium. However, as indicated in the bibliography, I have leaned heavily on monographic and floristic works where available. Personal observations were made throughout the planalto of Santa Catarina in 1956-57 on a grant from the National Science Foundation. The coastal rain forest was studied in 1928-29 on a Sheldon Travelling Fellowship from Harvard University and in 1952 on grants from the Rockefeller Foundation and the Serviço Nacional de Malaria of Brazil. The two most recent expeditions were made jointly with the Herbário "Barbosa Rodrigues" of Santa Catarina.

Unless otherwise indicated, the maps shown in this paper are based on the Goode base map No. 103, copyright 1937 by the University of Chicago.

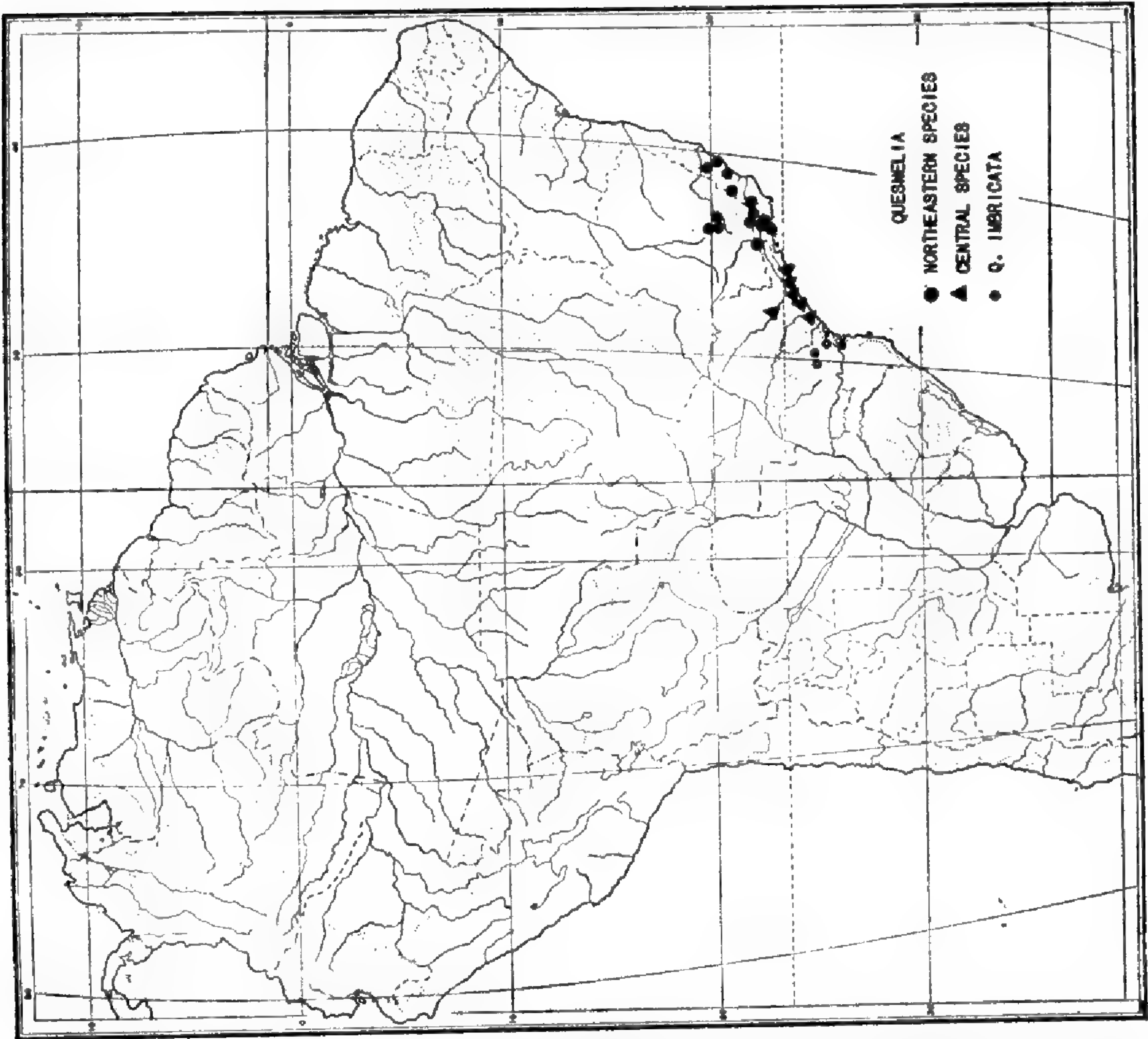


FIGURE 7.—Rain forest migration: *Quesnelia*.

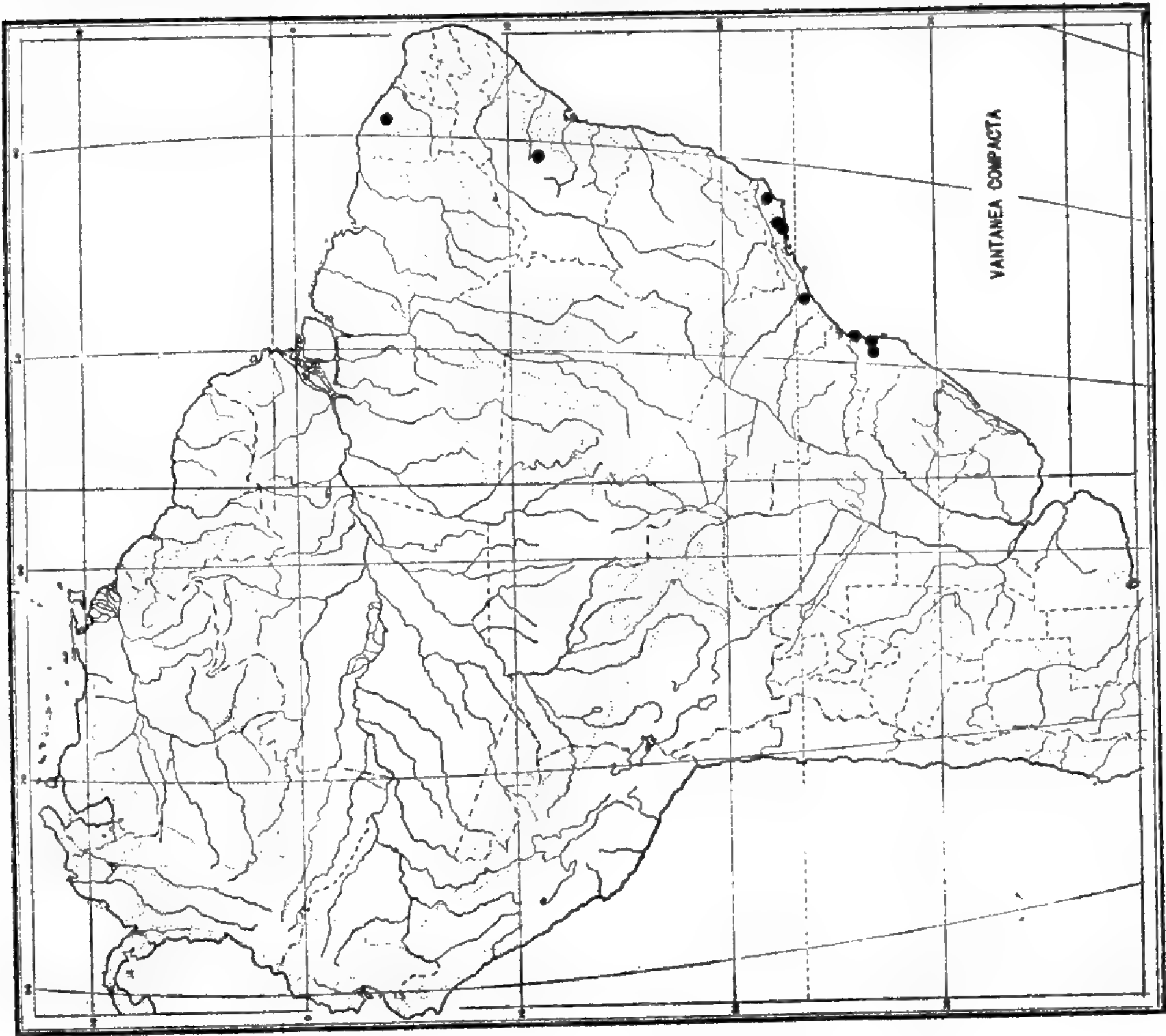


FIGURE 6.—Rain forest migration: *Vantanea compacta*.

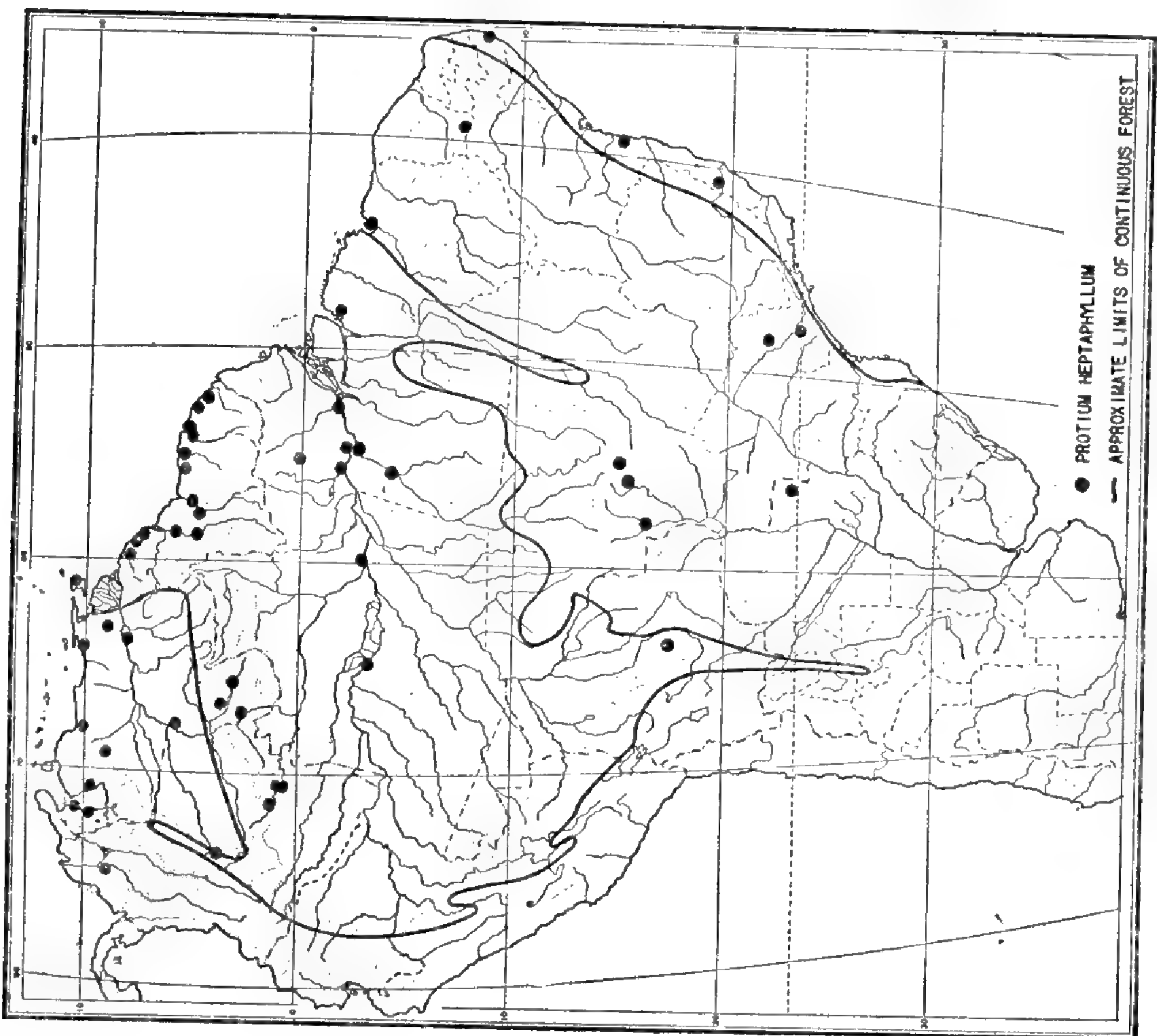


FIGURE 8.—Recent Amazonian migration: *Protium heptaphyllum*.

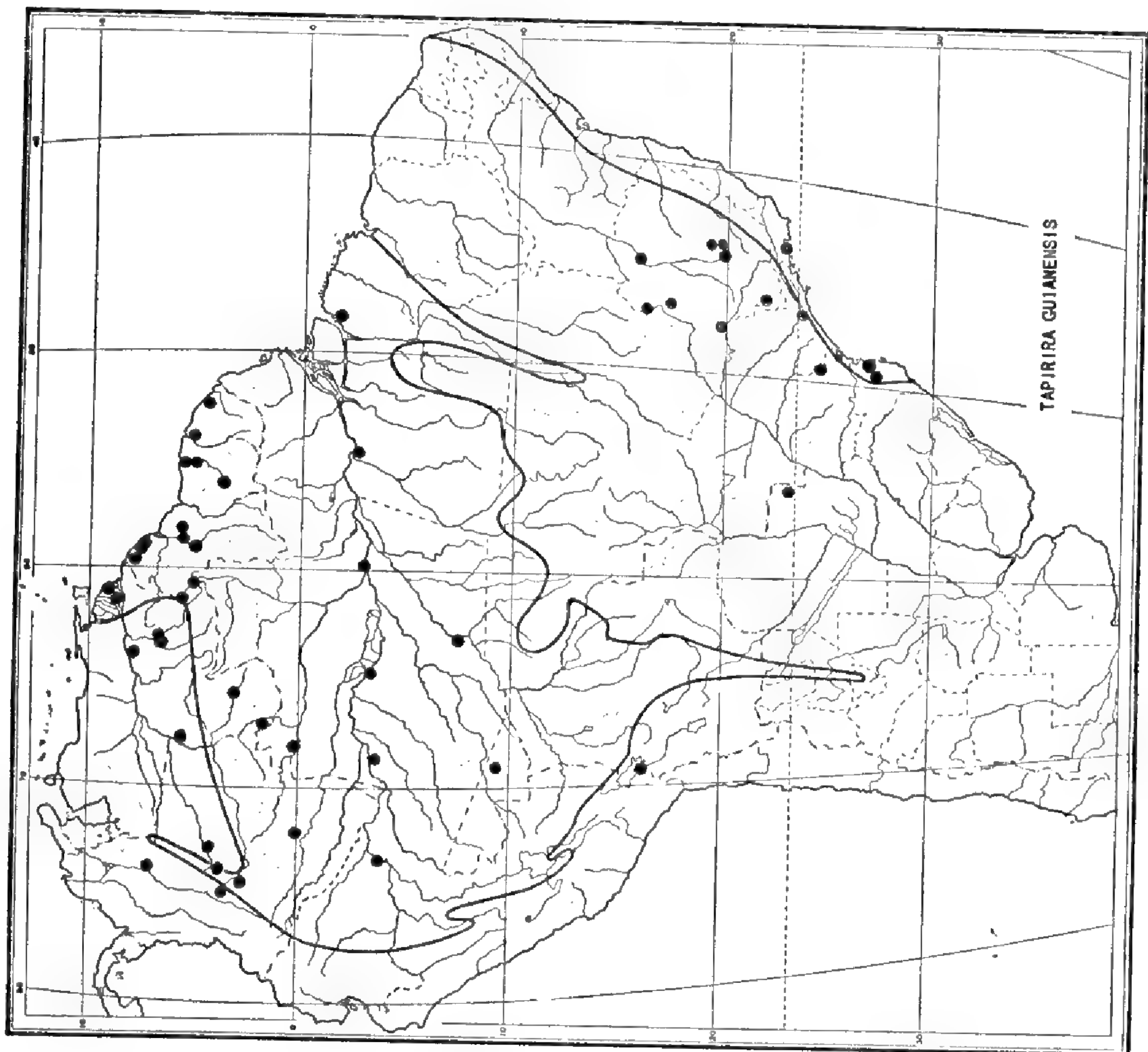


FIGURE 9.—Recent Amazonian migration: *Tapirira guianensis*.

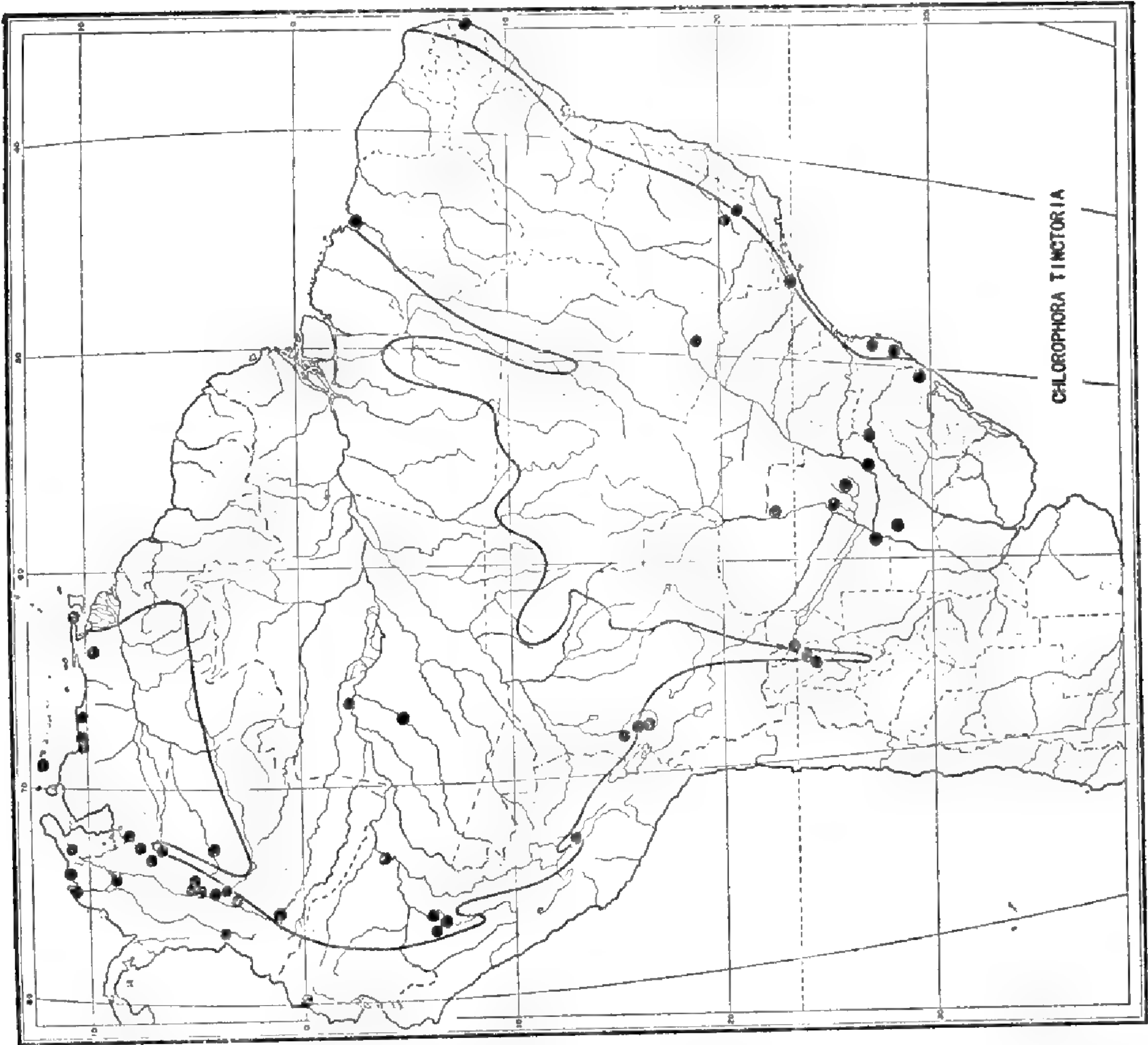


FIGURE 11.—Amazonian-Andean migration: *Chlorophora tinctoria*.

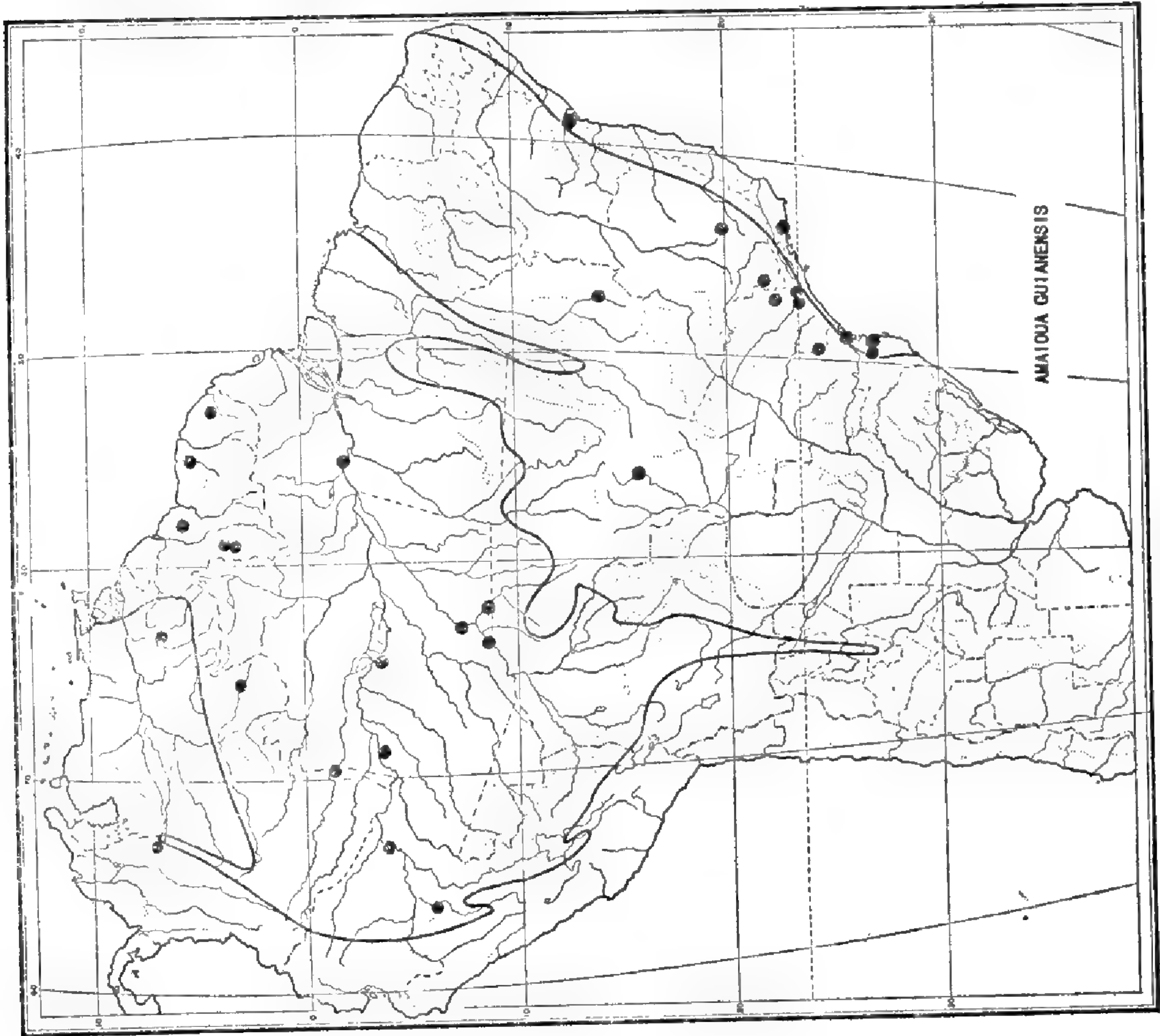
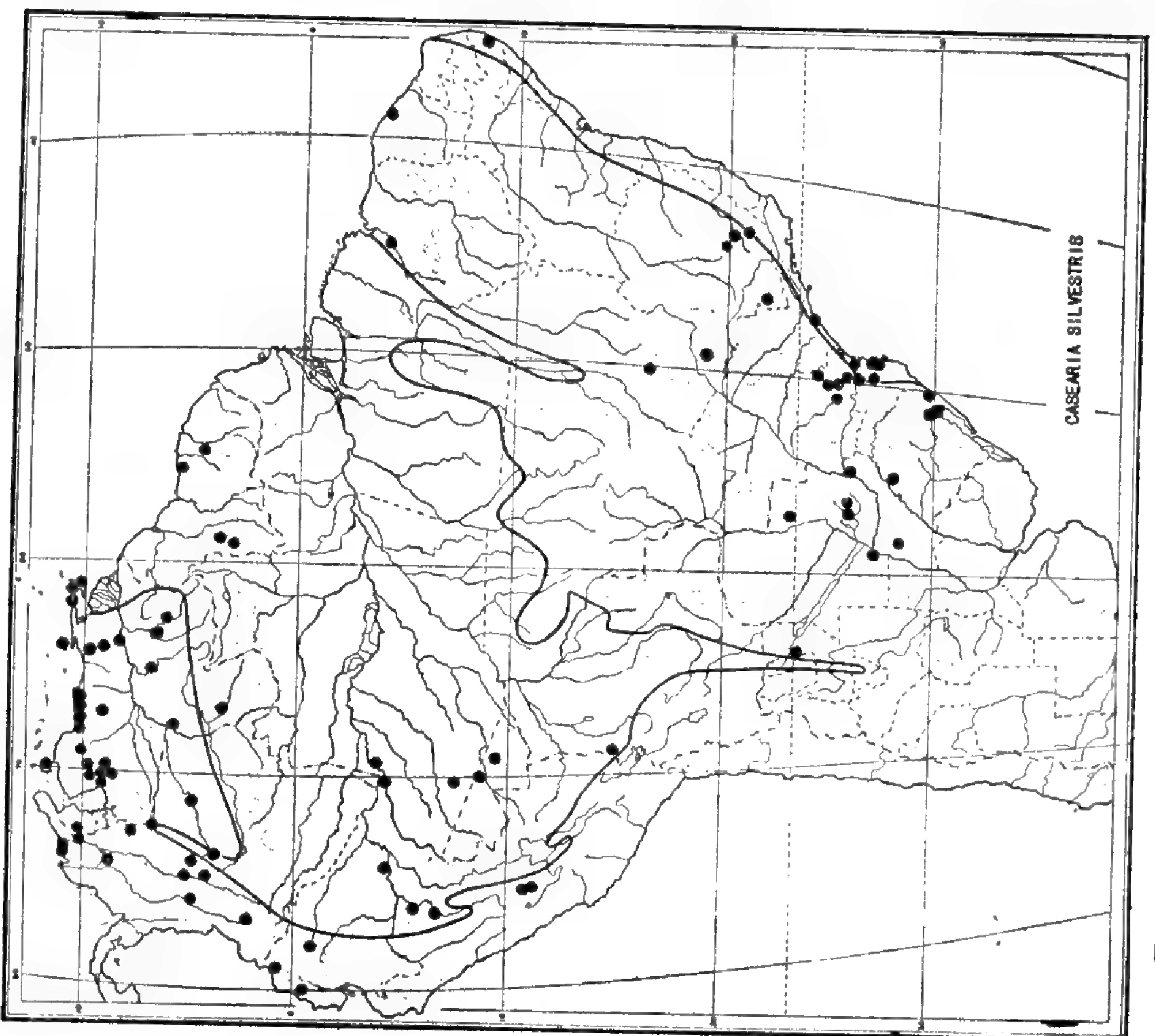
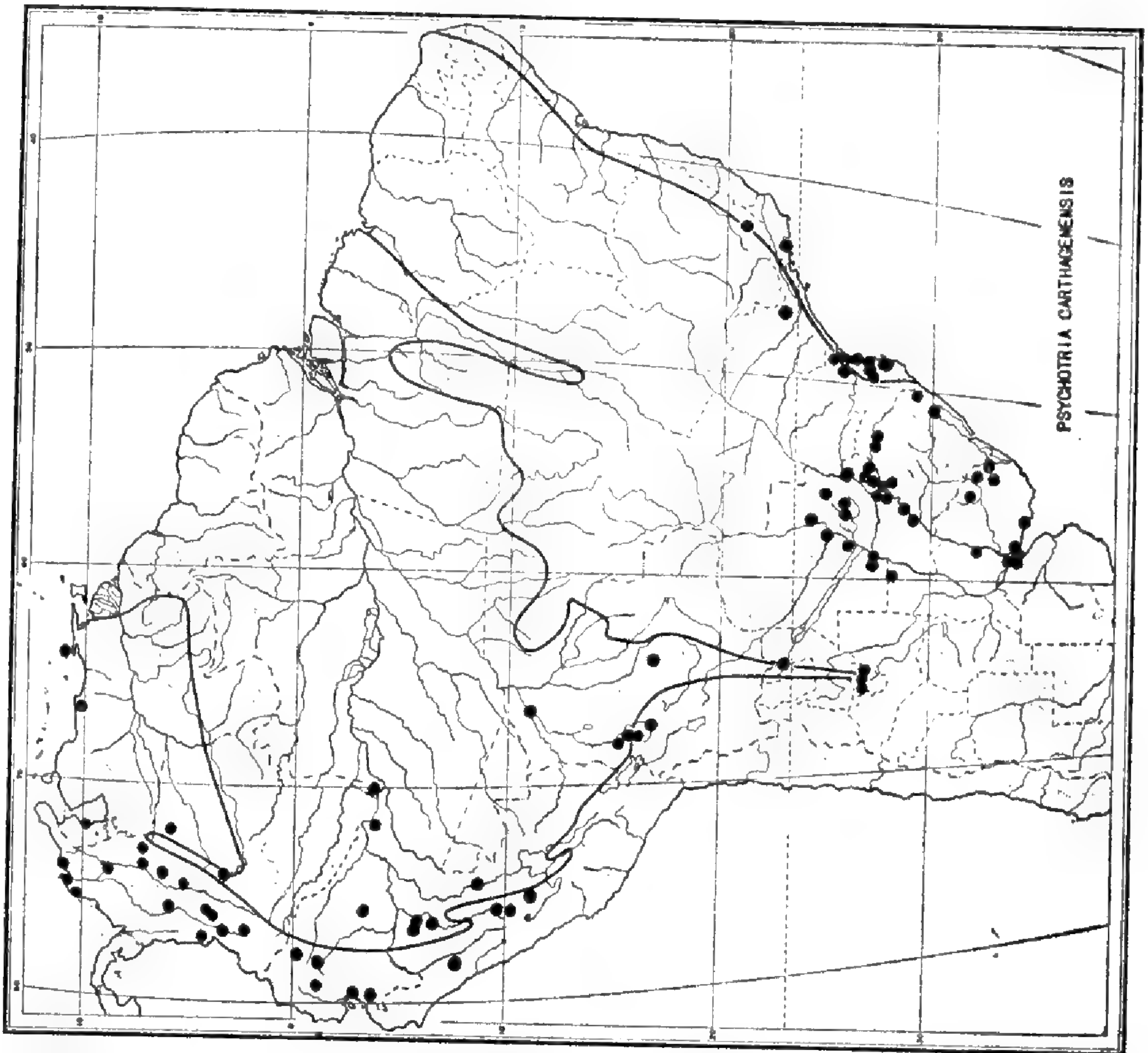


FIGURE 10.—Recent Amazonian migration: *Amaioua guianensis*.

FIGURE 12.—Amazonian-Andean migration: *Casearia silvestris*.FIGURE 13.—Amazonian-Andean migration: *Psychotria carthagenensis*.

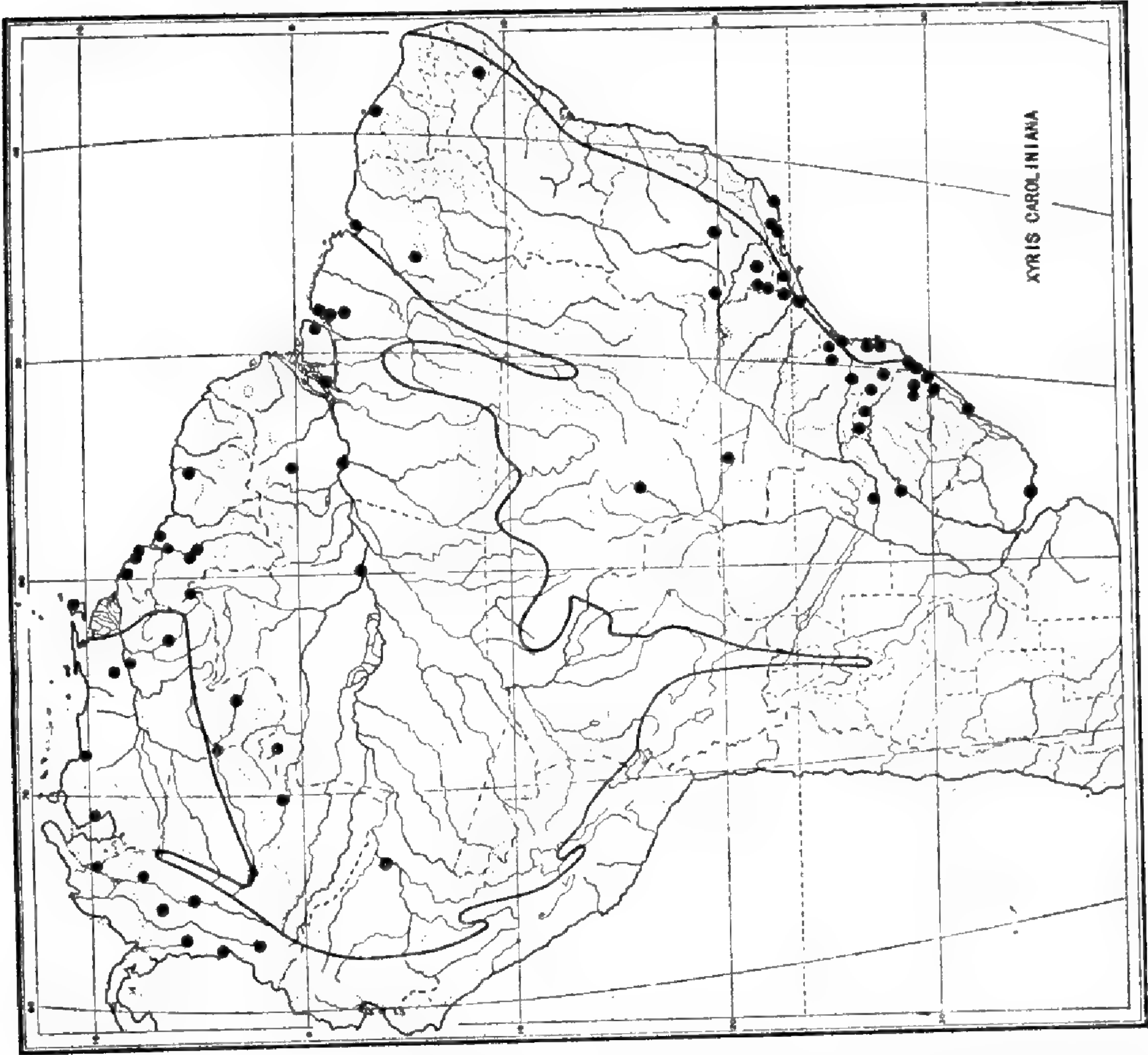


FIGURE 15.—Ruderal migration: *Xyris caroliniana*.

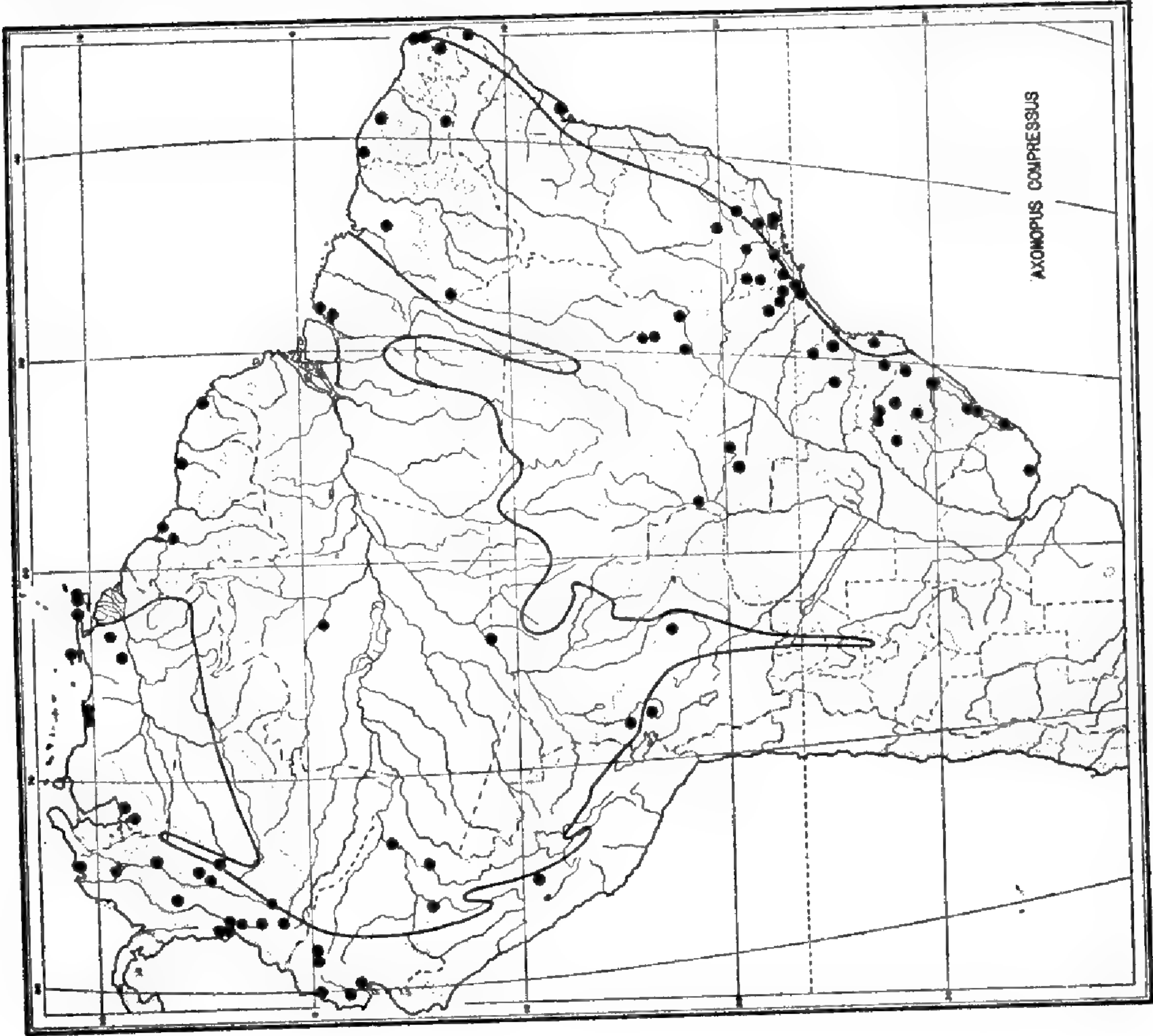


FIGURE 14.—Ruderal migration: *Axonopus compressus*.

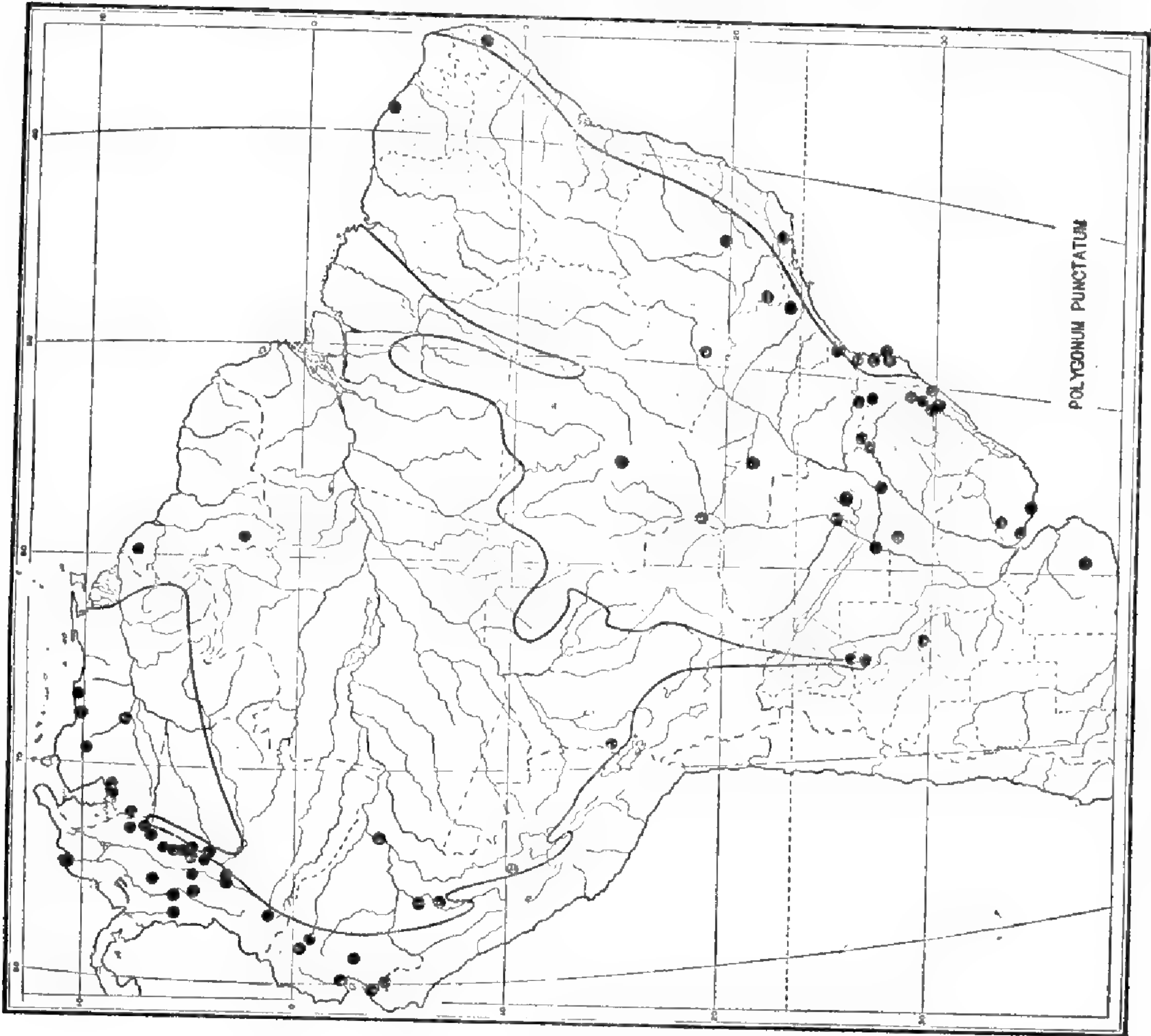


FIGURE 16.—Ruderal migration: *Polygonum punctatum*.

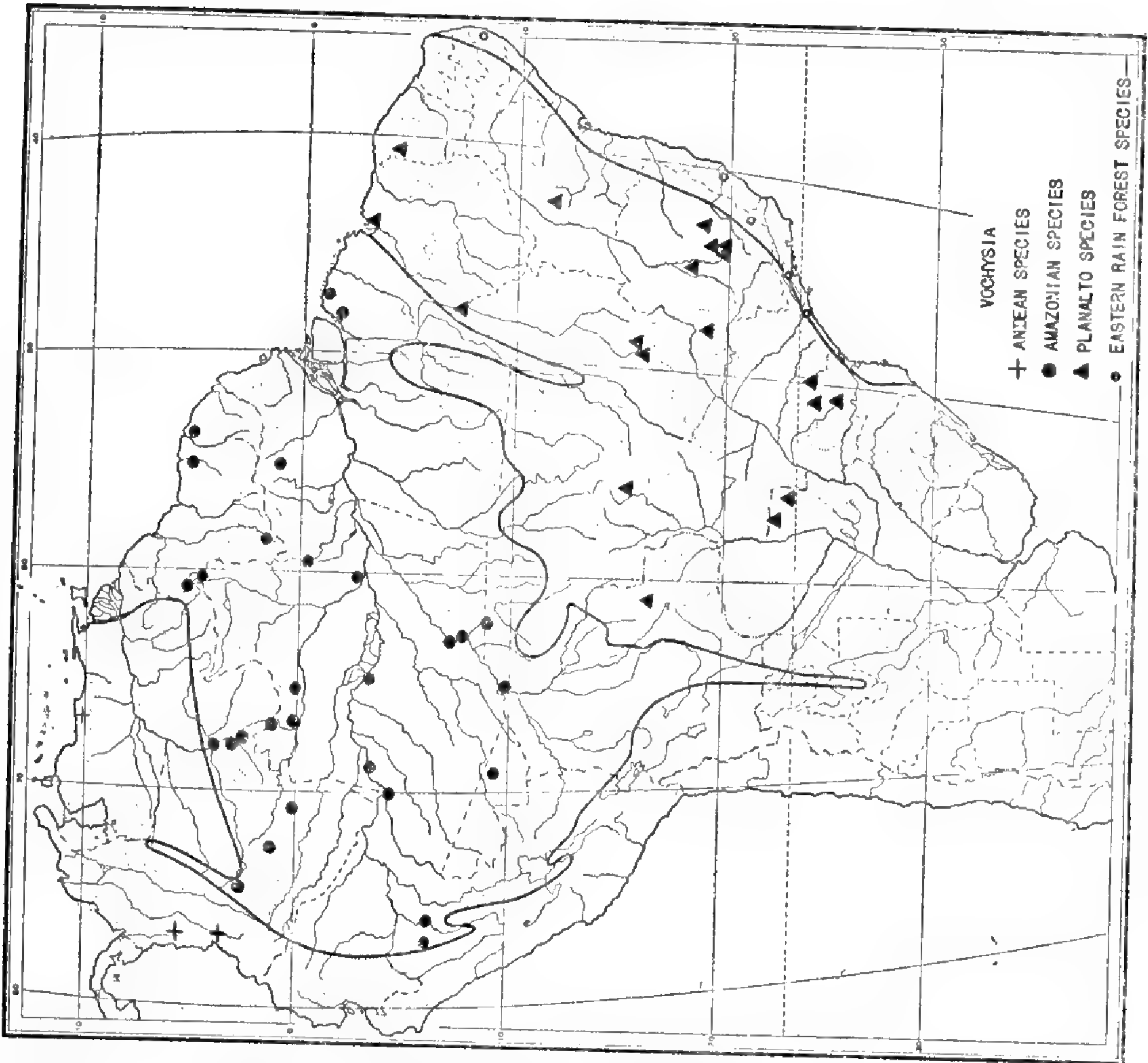
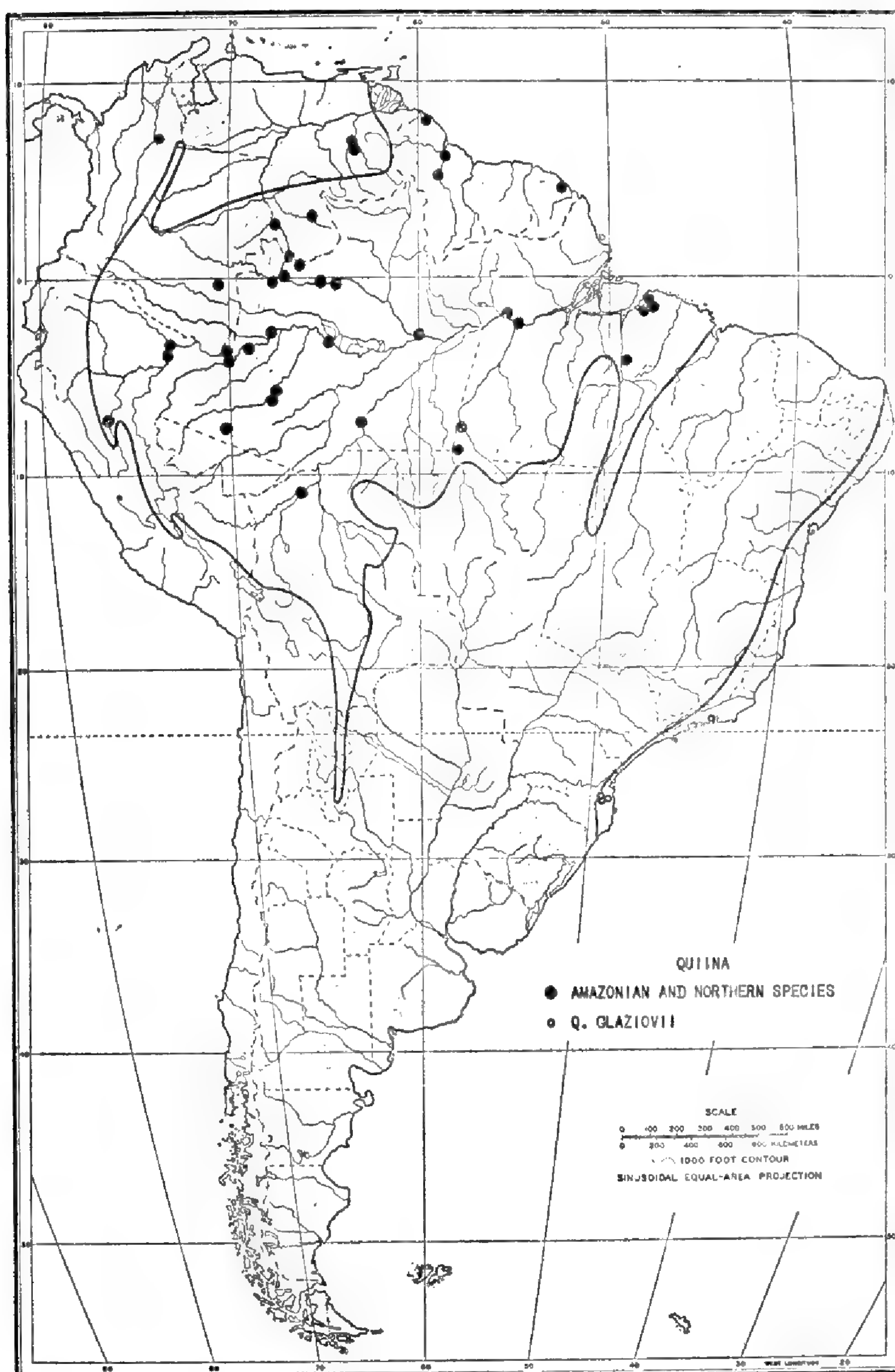


FIGURE 17.—Ancient Amazonian migration: *Vochysia*.

FIGURE 18.—Ancient Amazonian migration: *Quiina*.

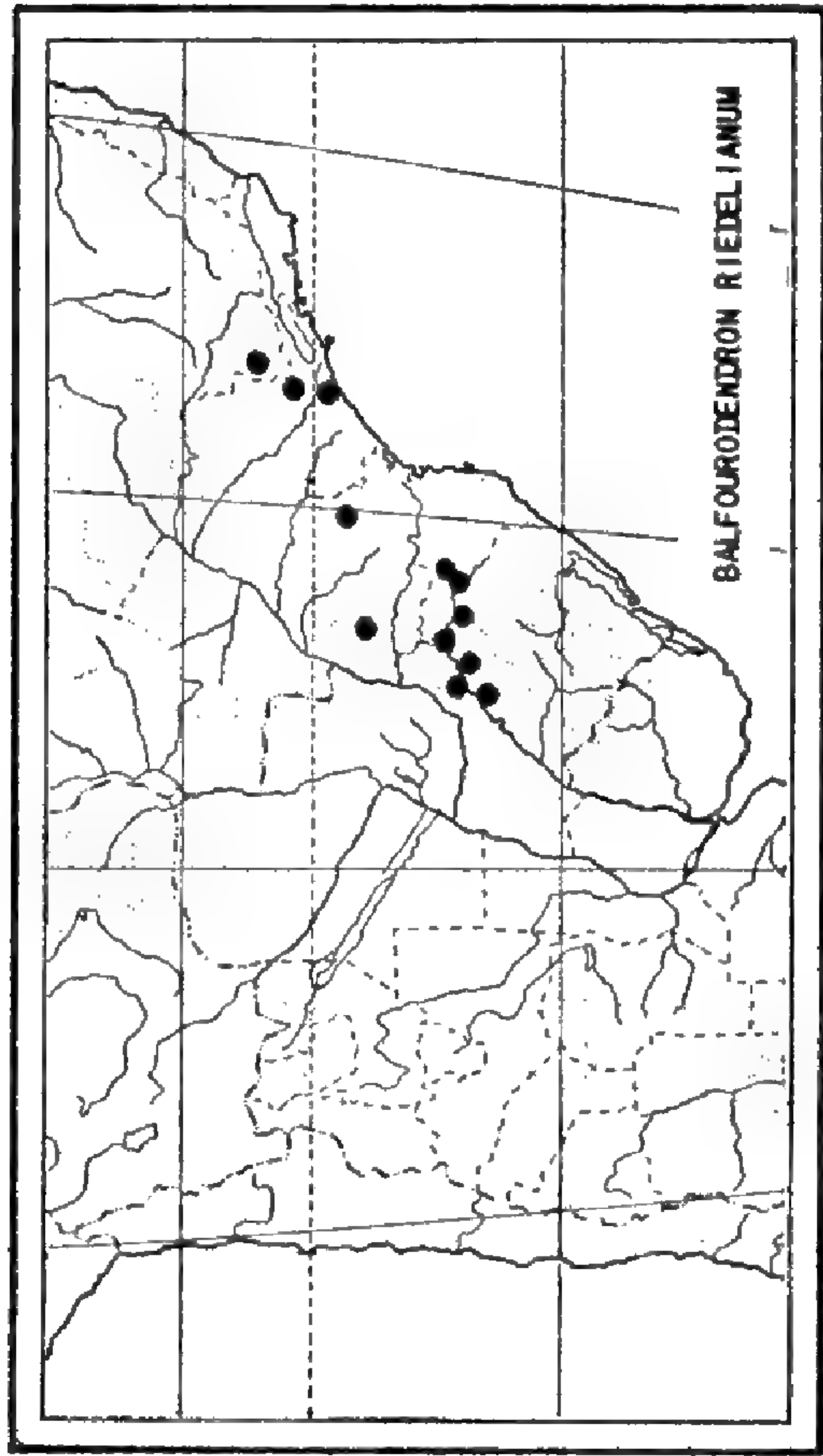


FIGURE 20.—Paraguayan migration: *Balfourodendron riedelianum*.

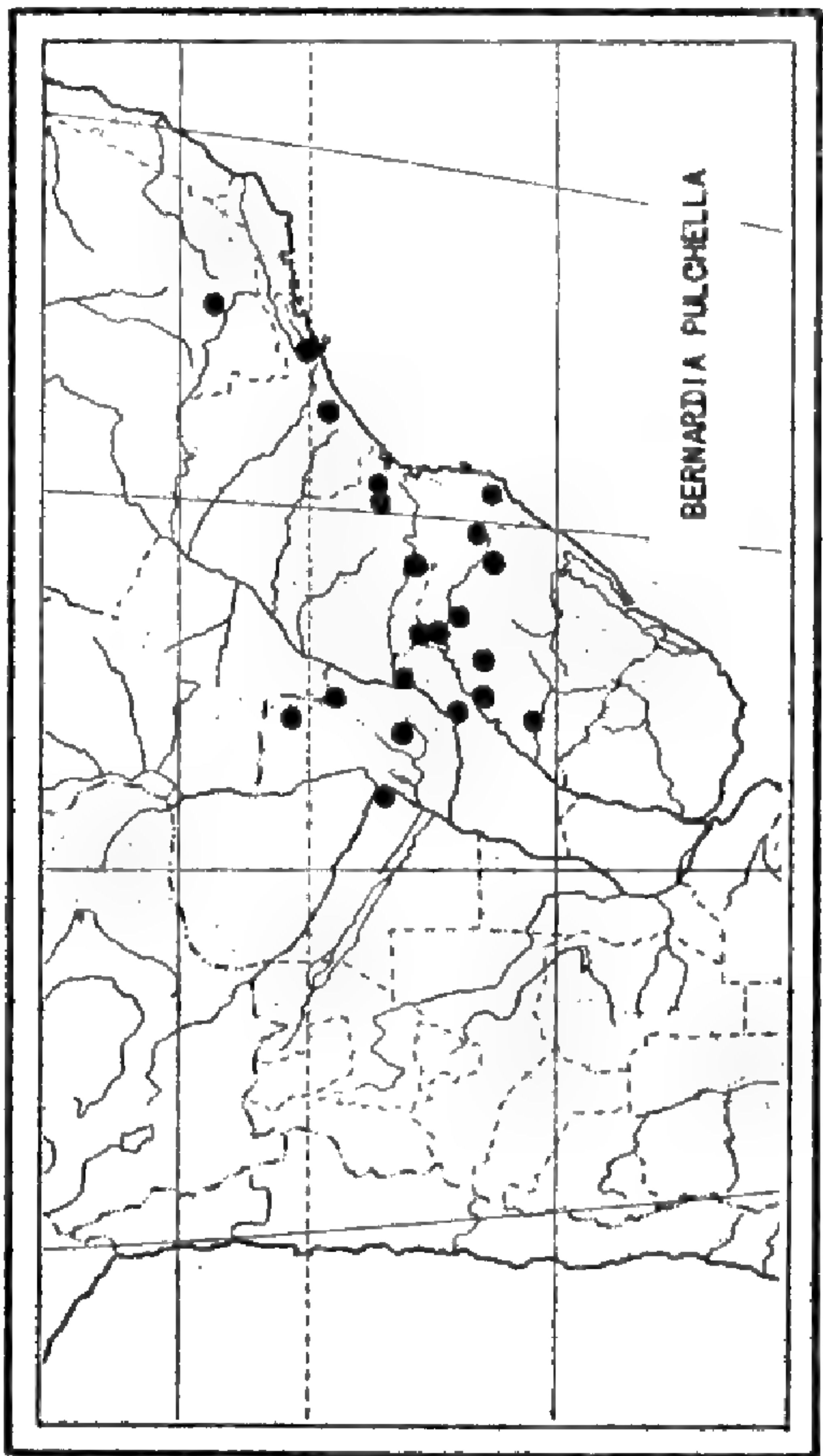


FIGURE 22.—Paraguayan migration: *Bernardia pulchella*.

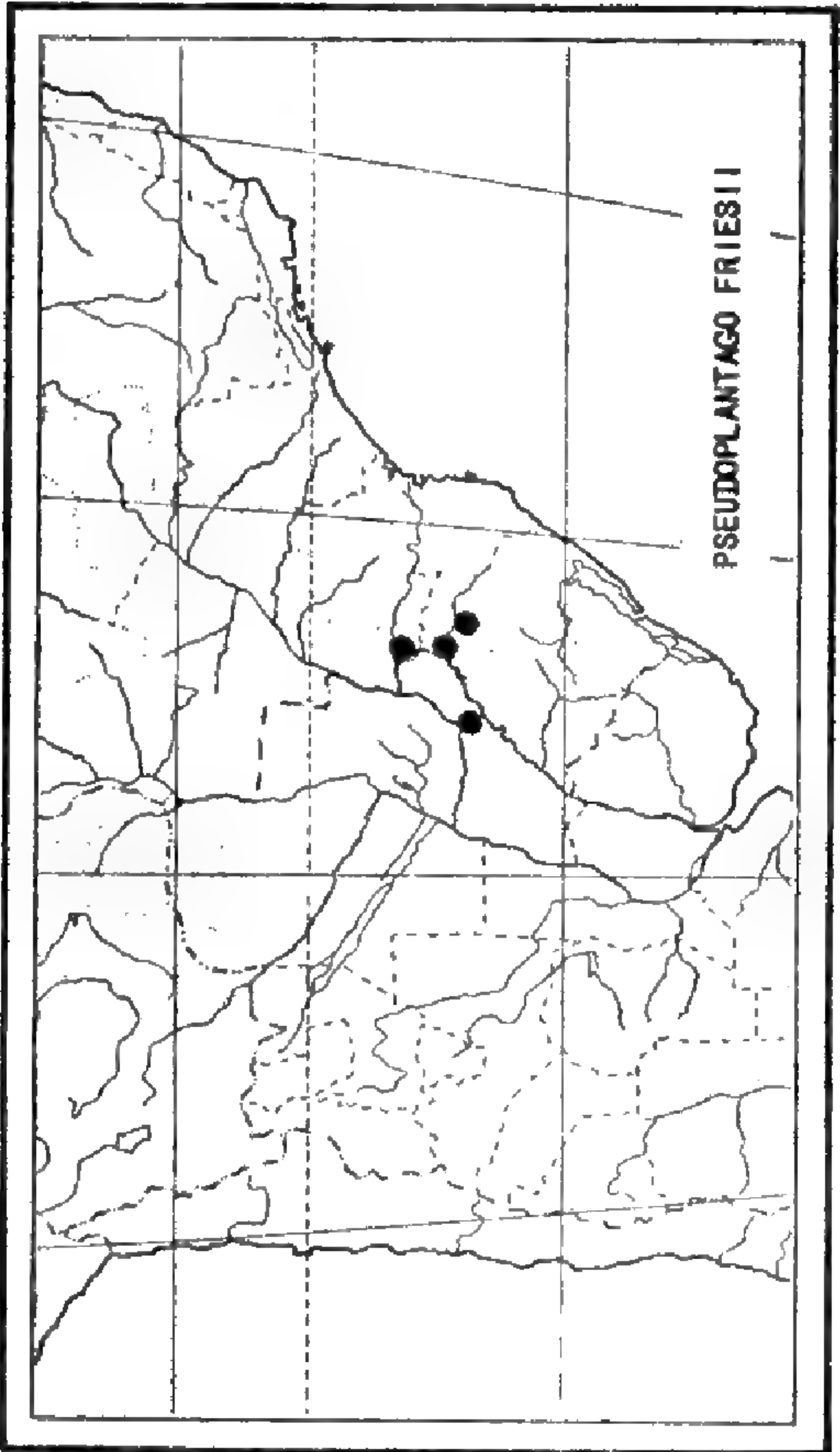


FIGURE 19.—Paraguayan migration: *Pseudoplantago friesii*.

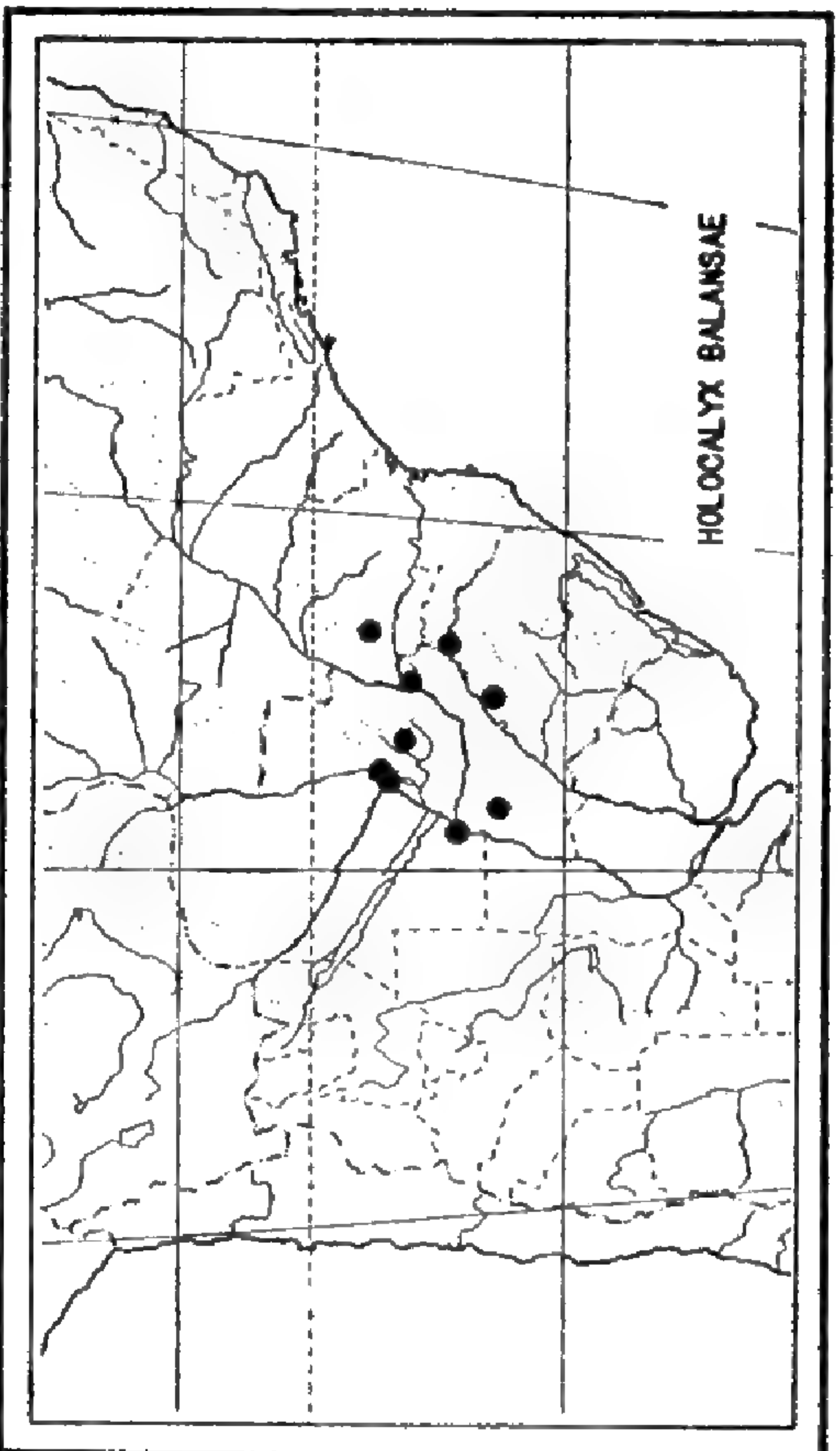


FIGURE 21.—Paraguayan migration: *Holocalyx balansae*.

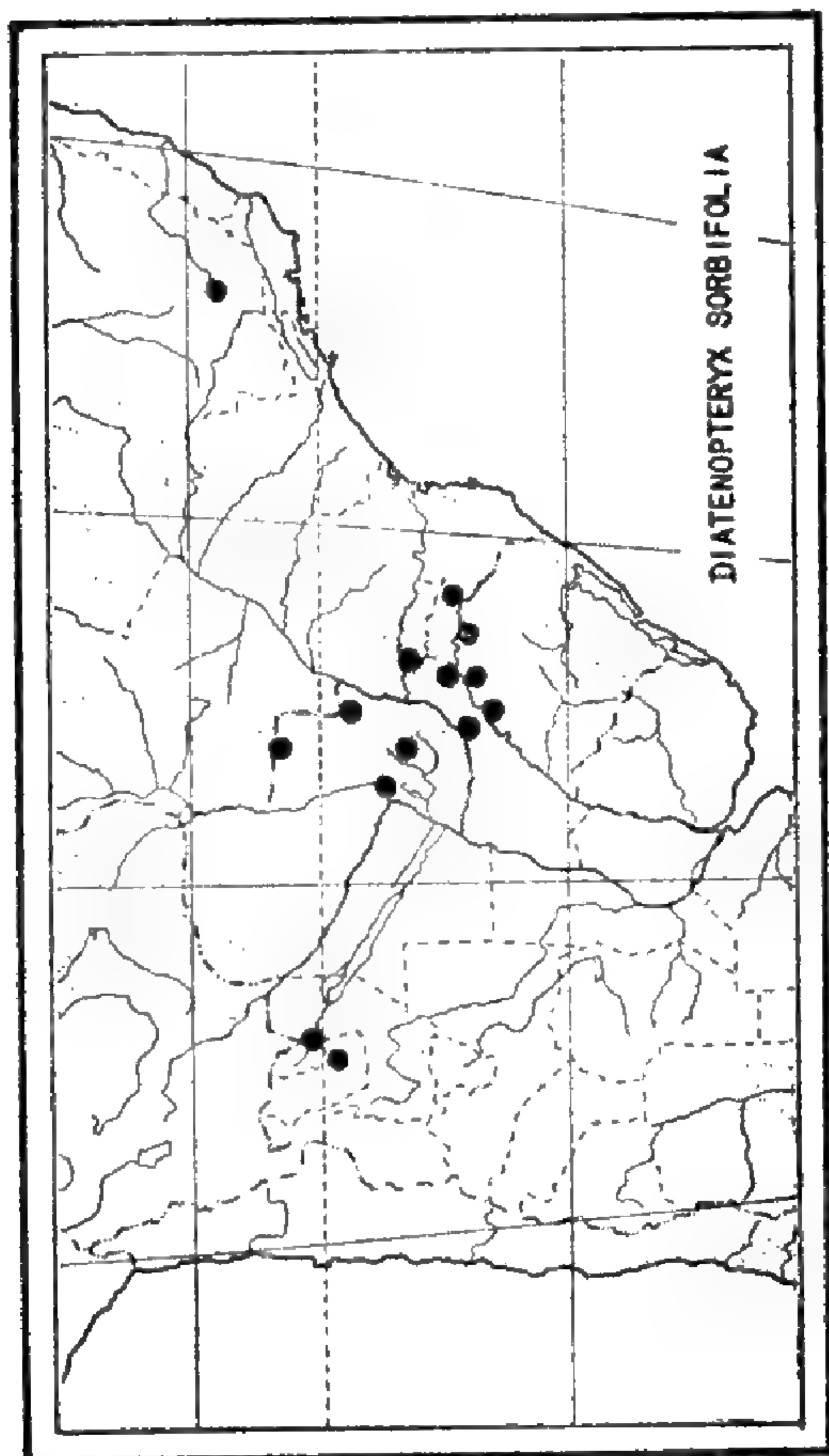


FIGURE 24.—Paraguayan migration: *Diatenoptyx sorbifolia*.

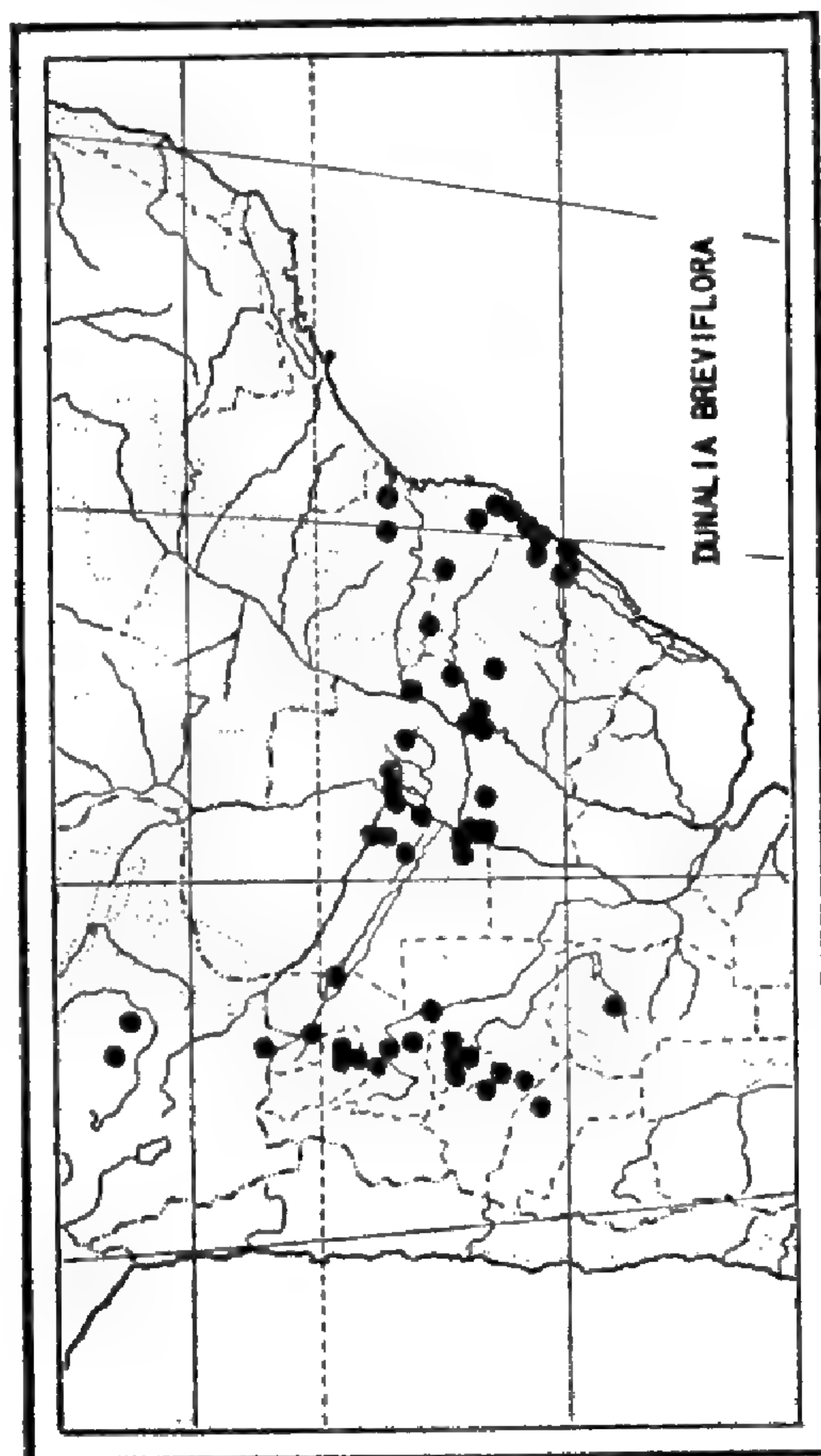


FIGURE 26.—Paraguayan migration: *Dunalia breviflora*.

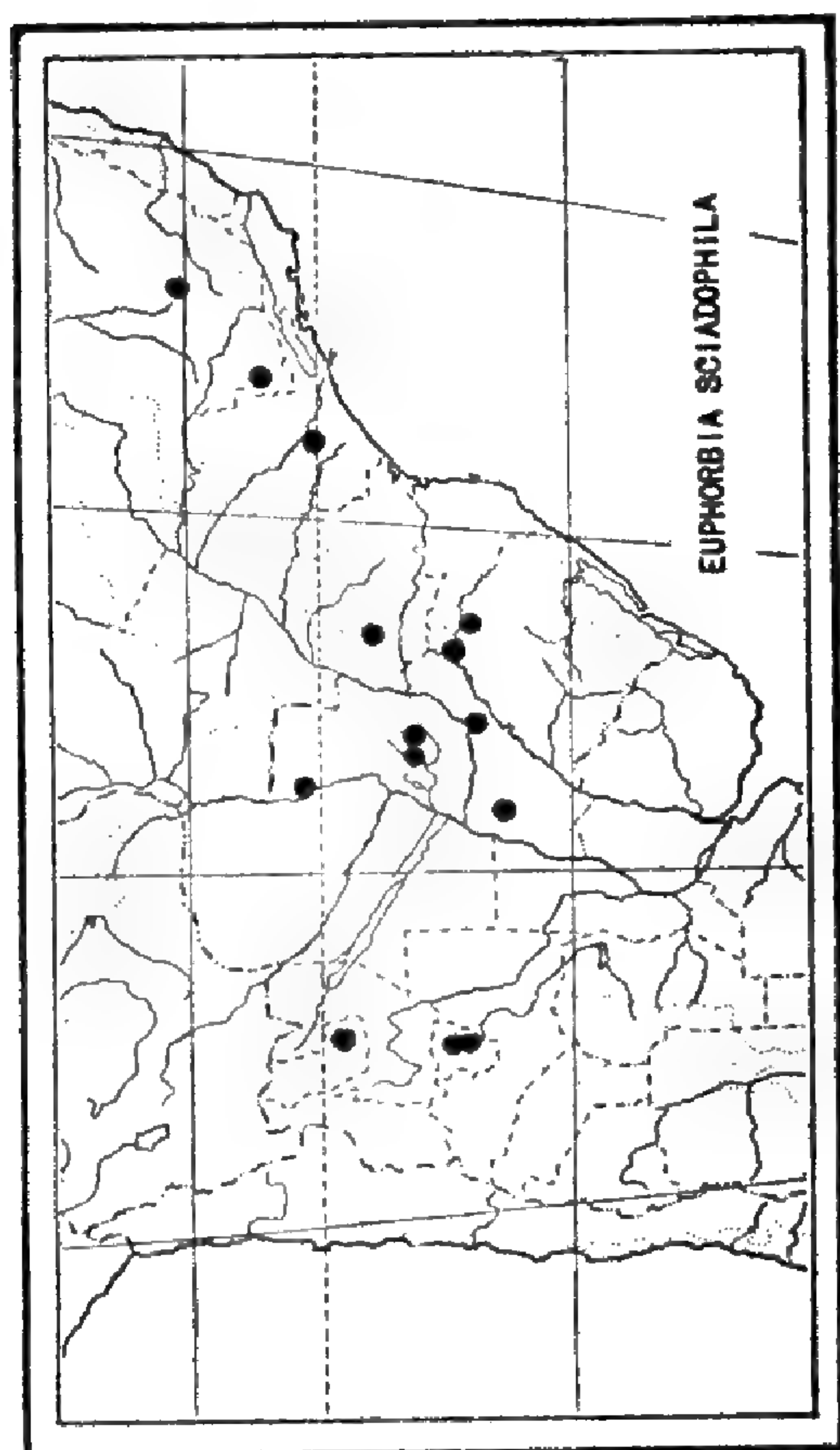


FIGURE 23.—Paraguayan migration: *Euphorbia sciadophila*.

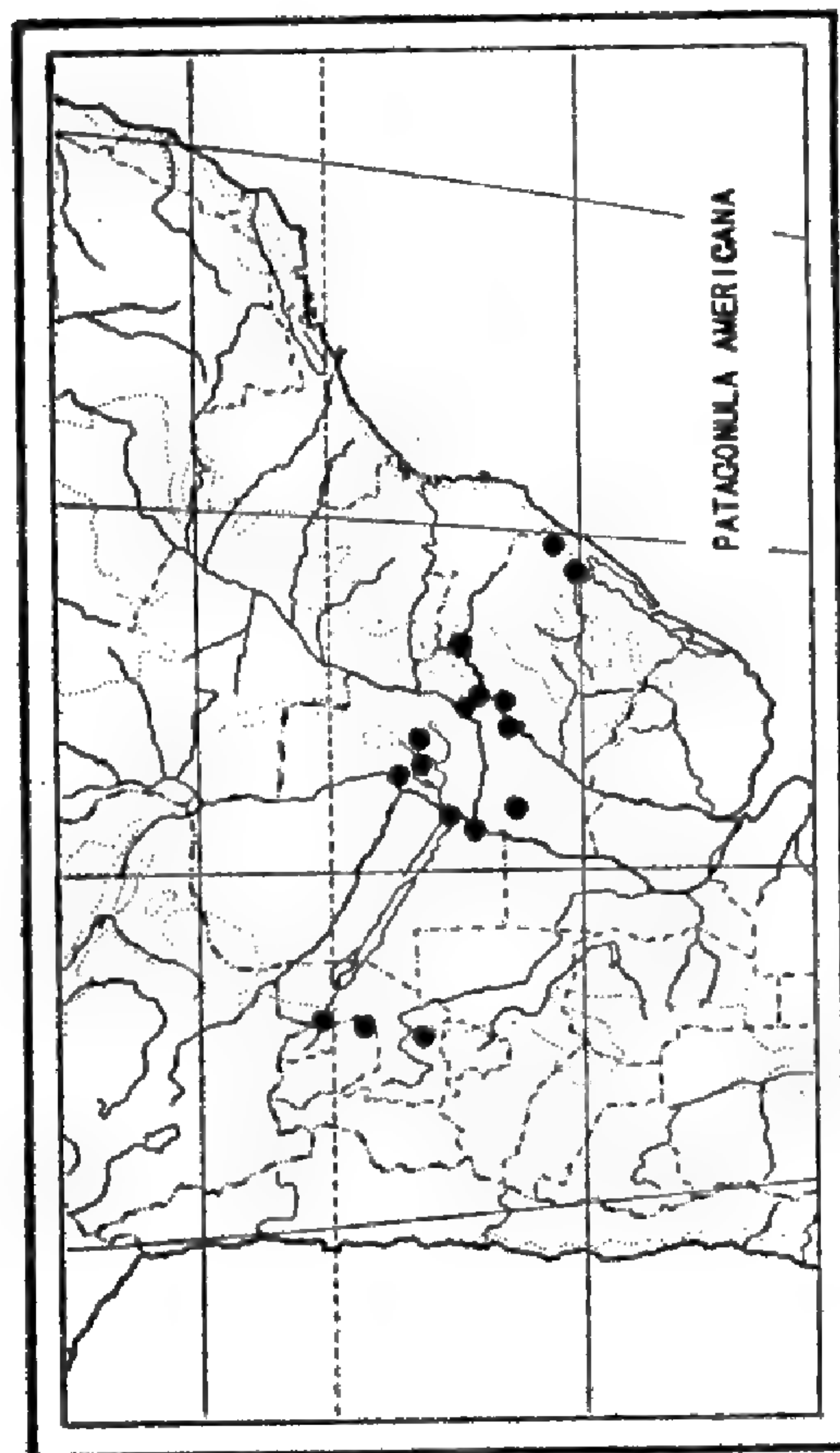


FIGURE 25.—Paraguayan migration: *Patagonula americana*.

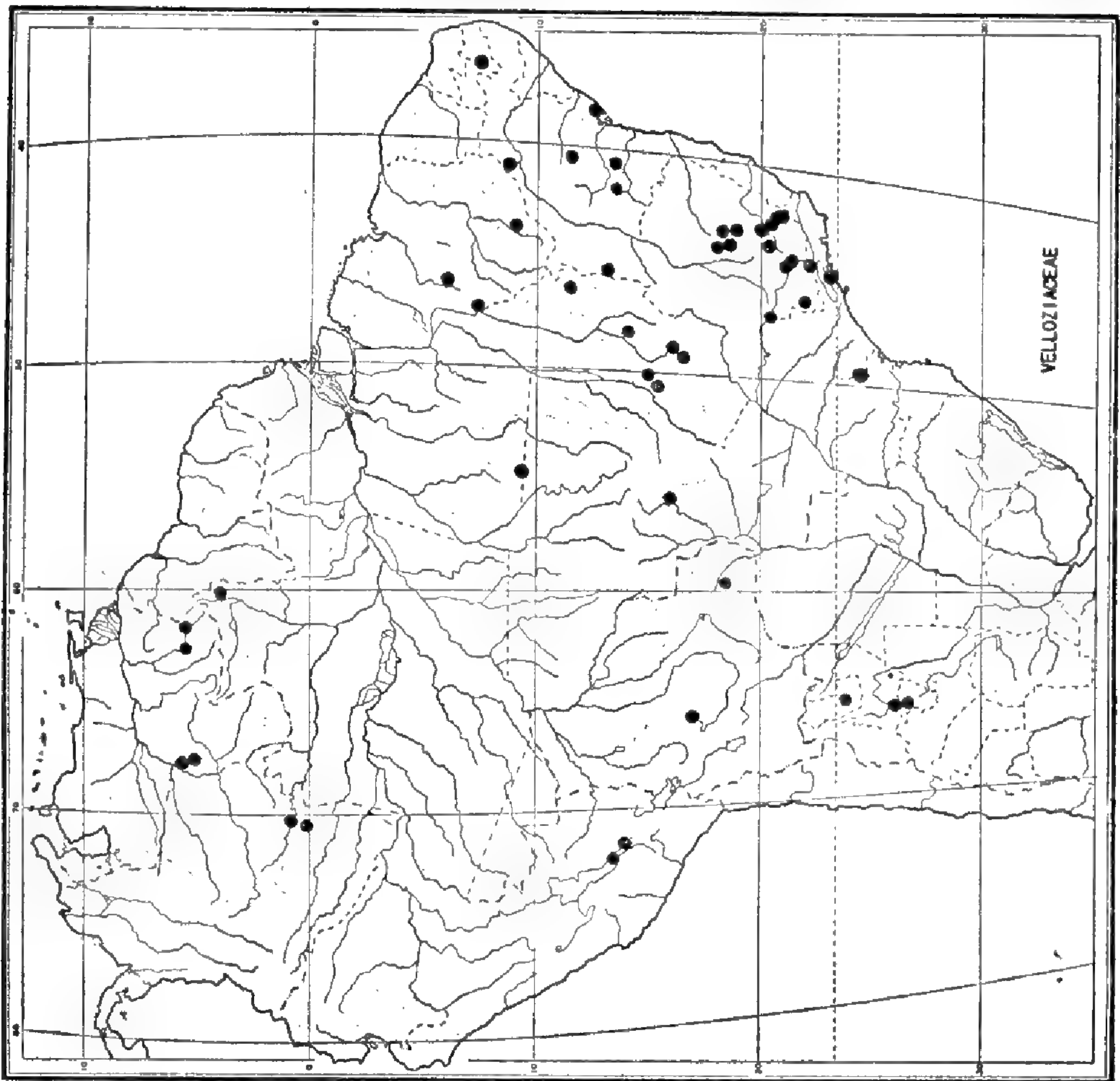


FIGURE 27.—Planalto migration: Velloziaceae.

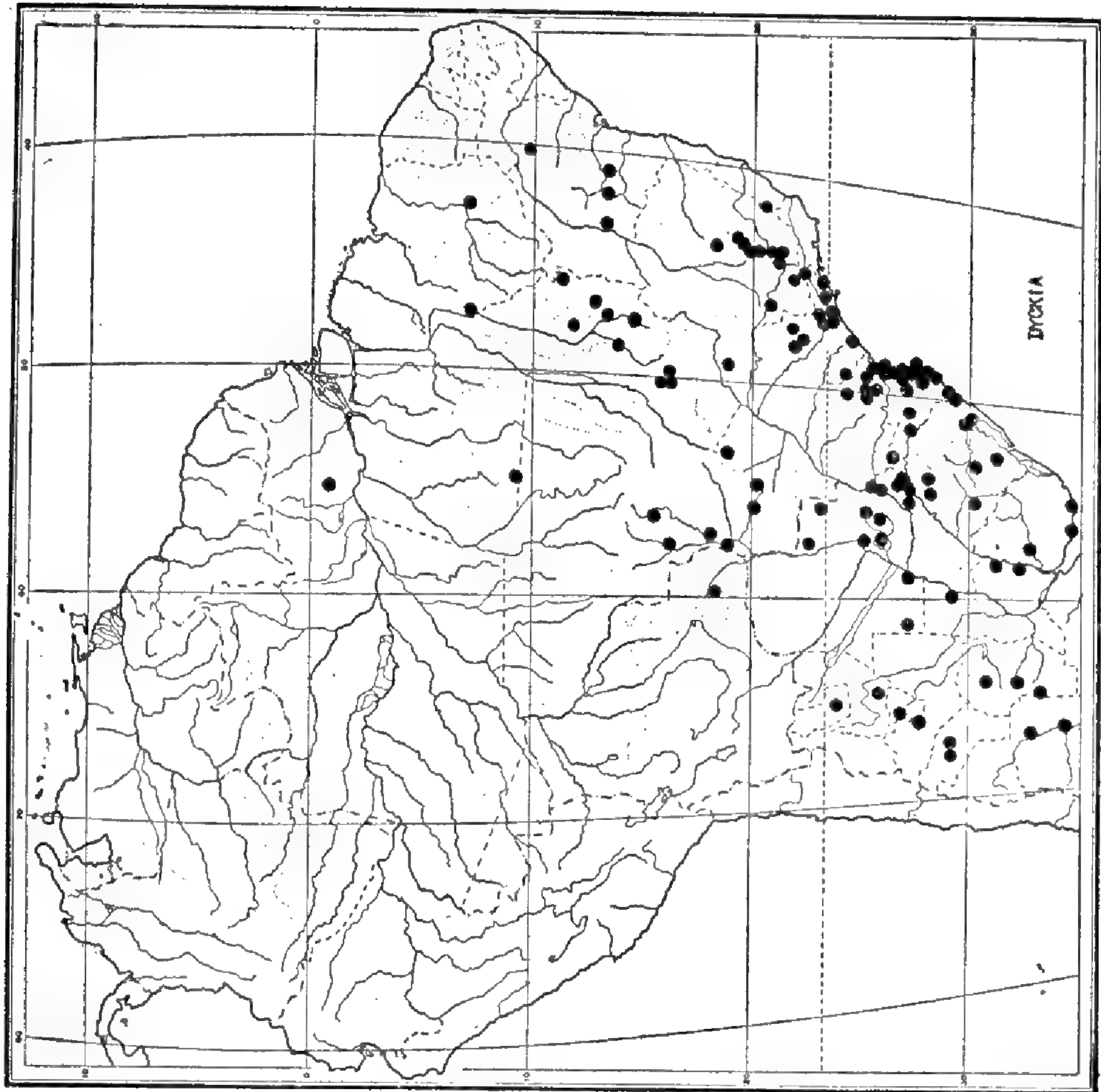
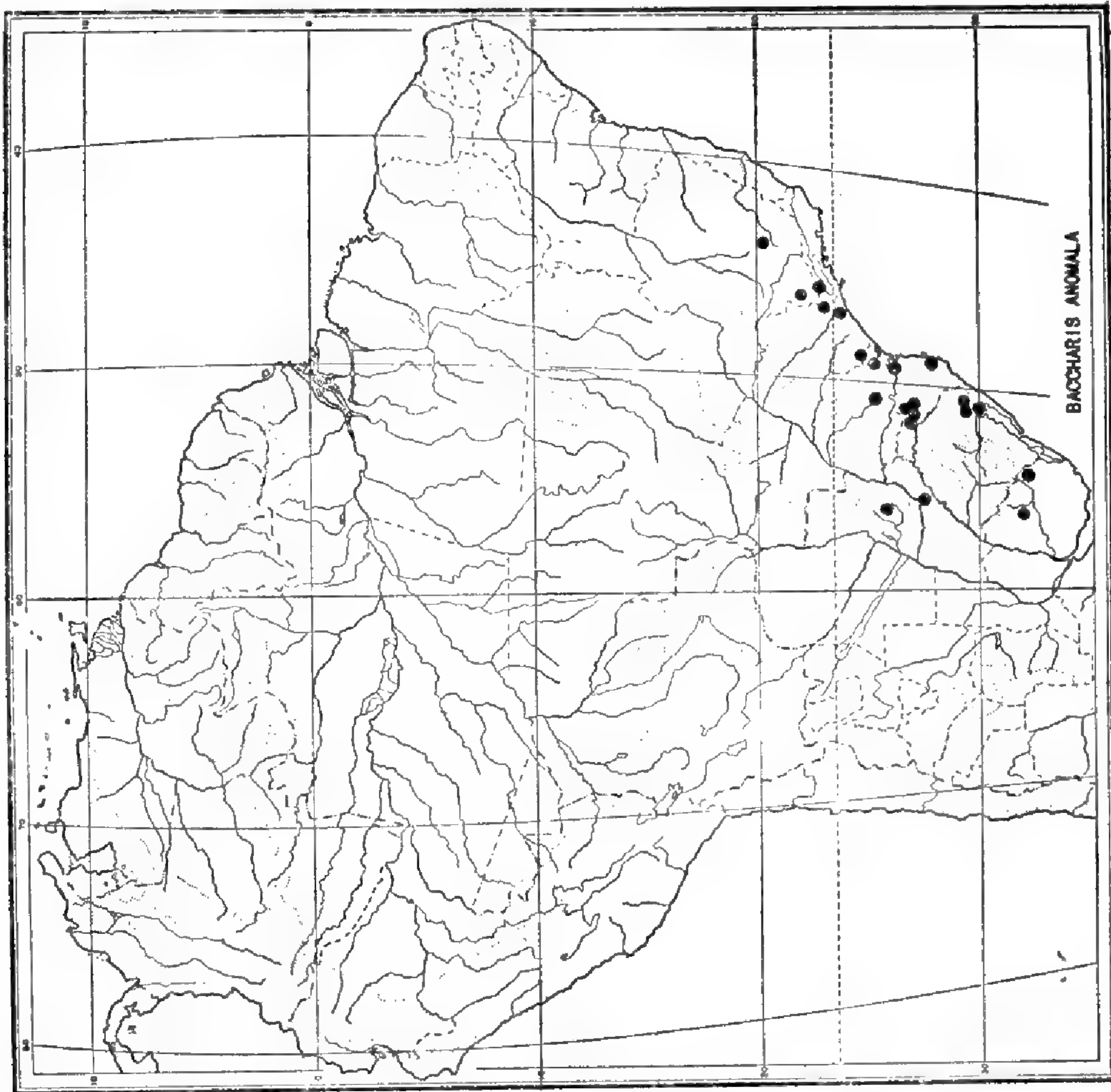
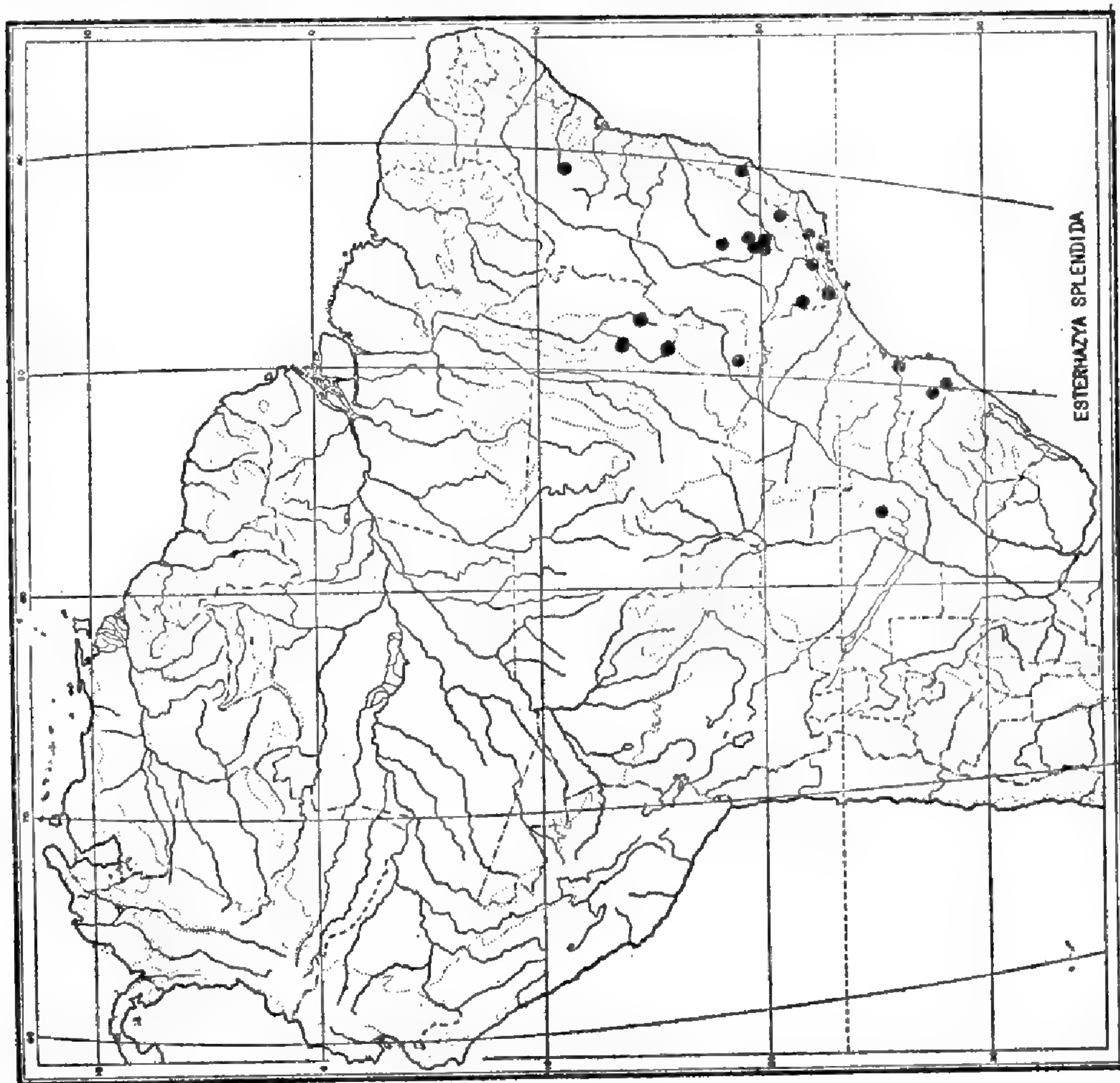


FIGURE 28.—Planalto migration: *Dyckia*.

FIGURE 30.—Planalto-coastal migration: *Baccharis anomala*.FIGURE 29.—Planalto-coastal migration: *Esterhazyia splendida*.

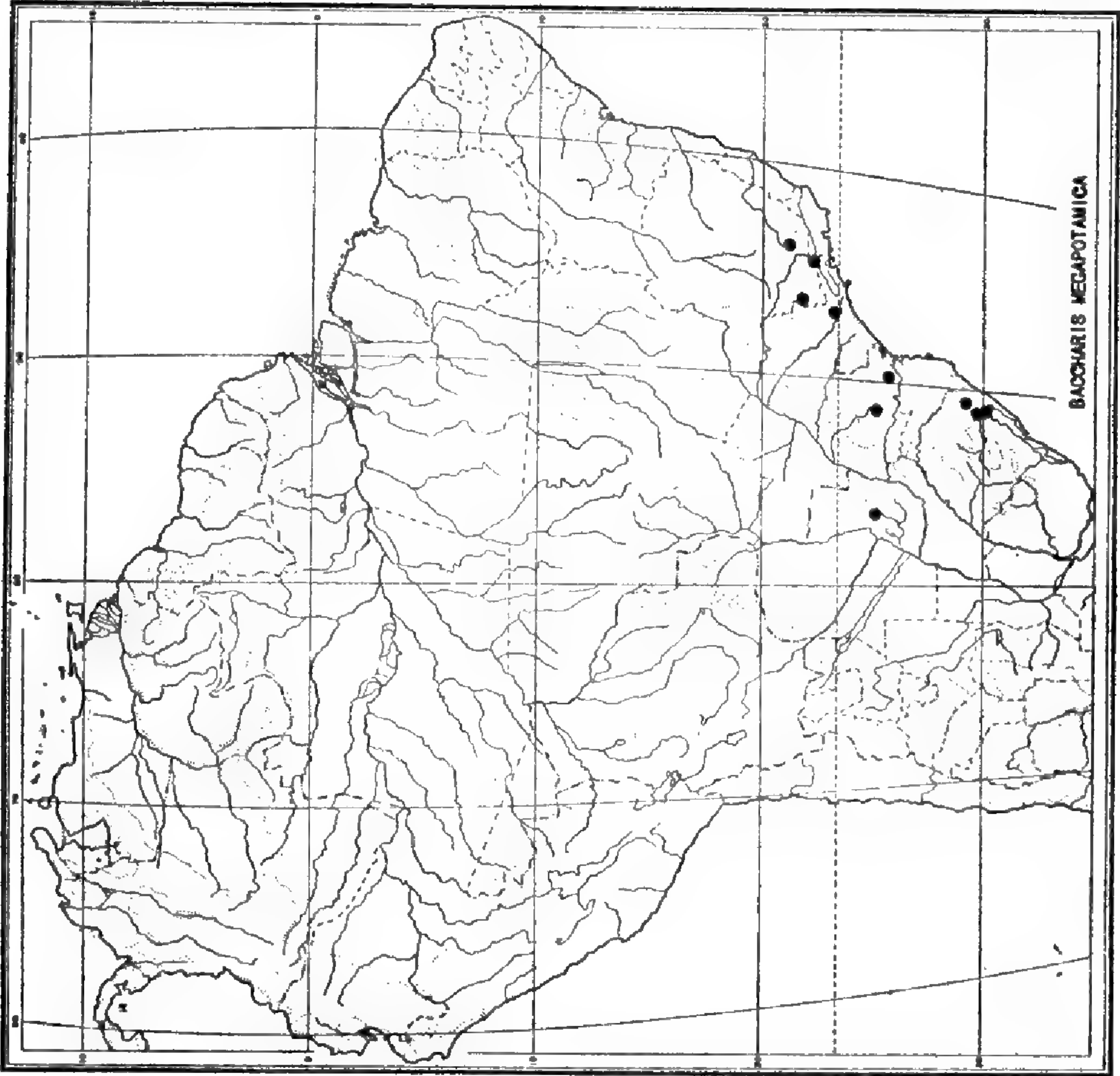


FIGURE 31.—Planalto migration: *Baccharis megapotamica*.

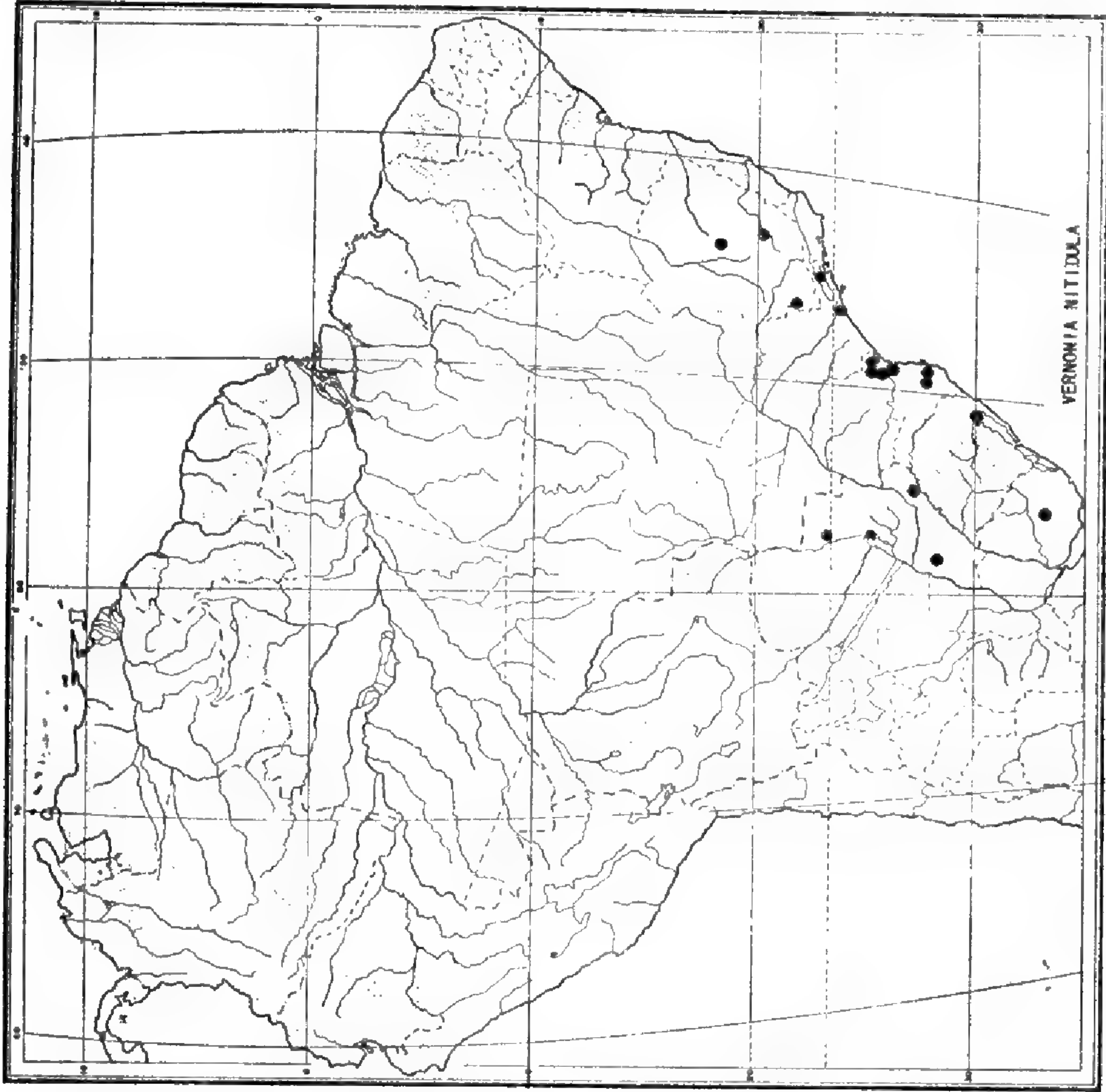


FIGURE 32.—Planalto-coastal migration: *Vernonia nitidula*.

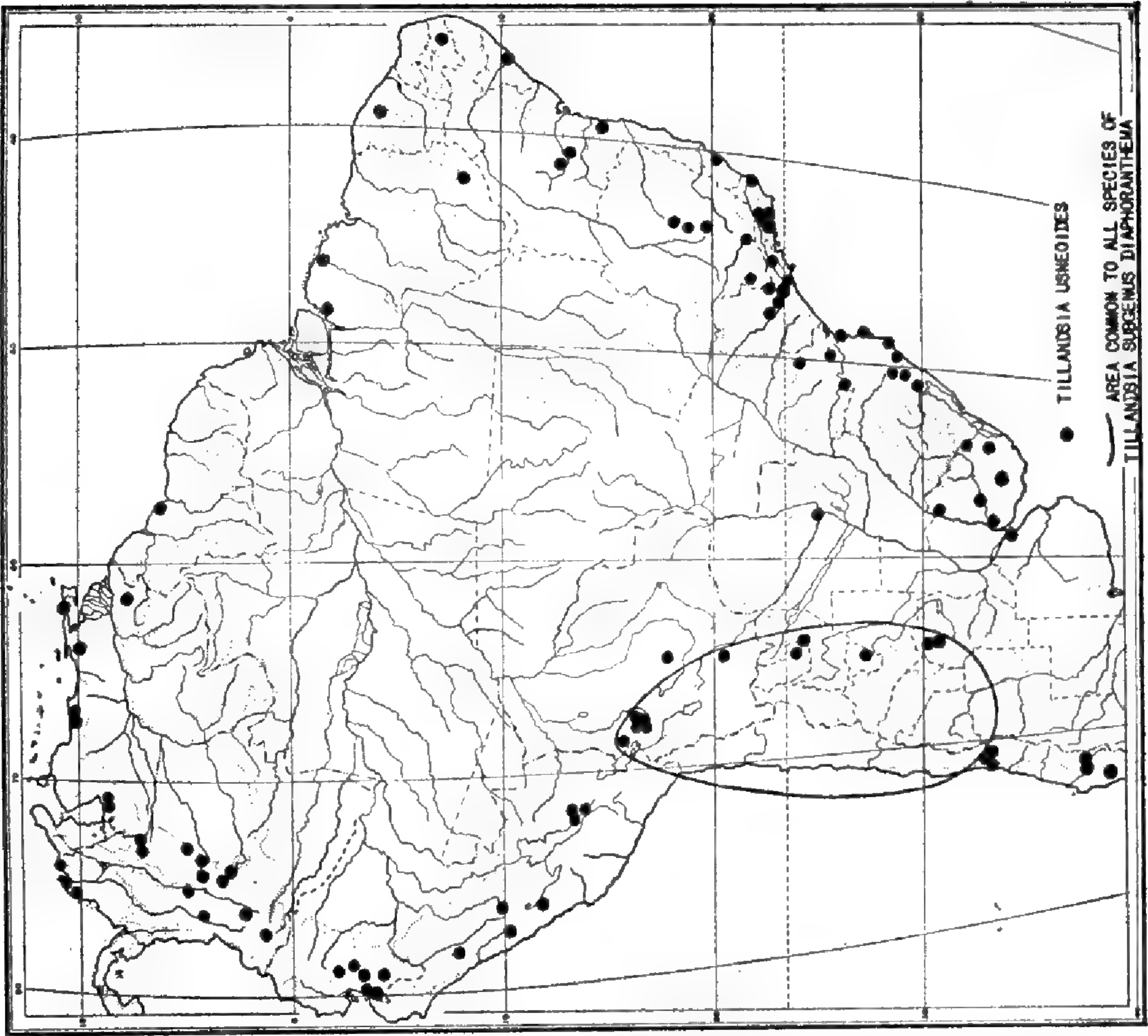


FIGURE 34.—Recent Andean migration: *Tillandsia usneoides*.

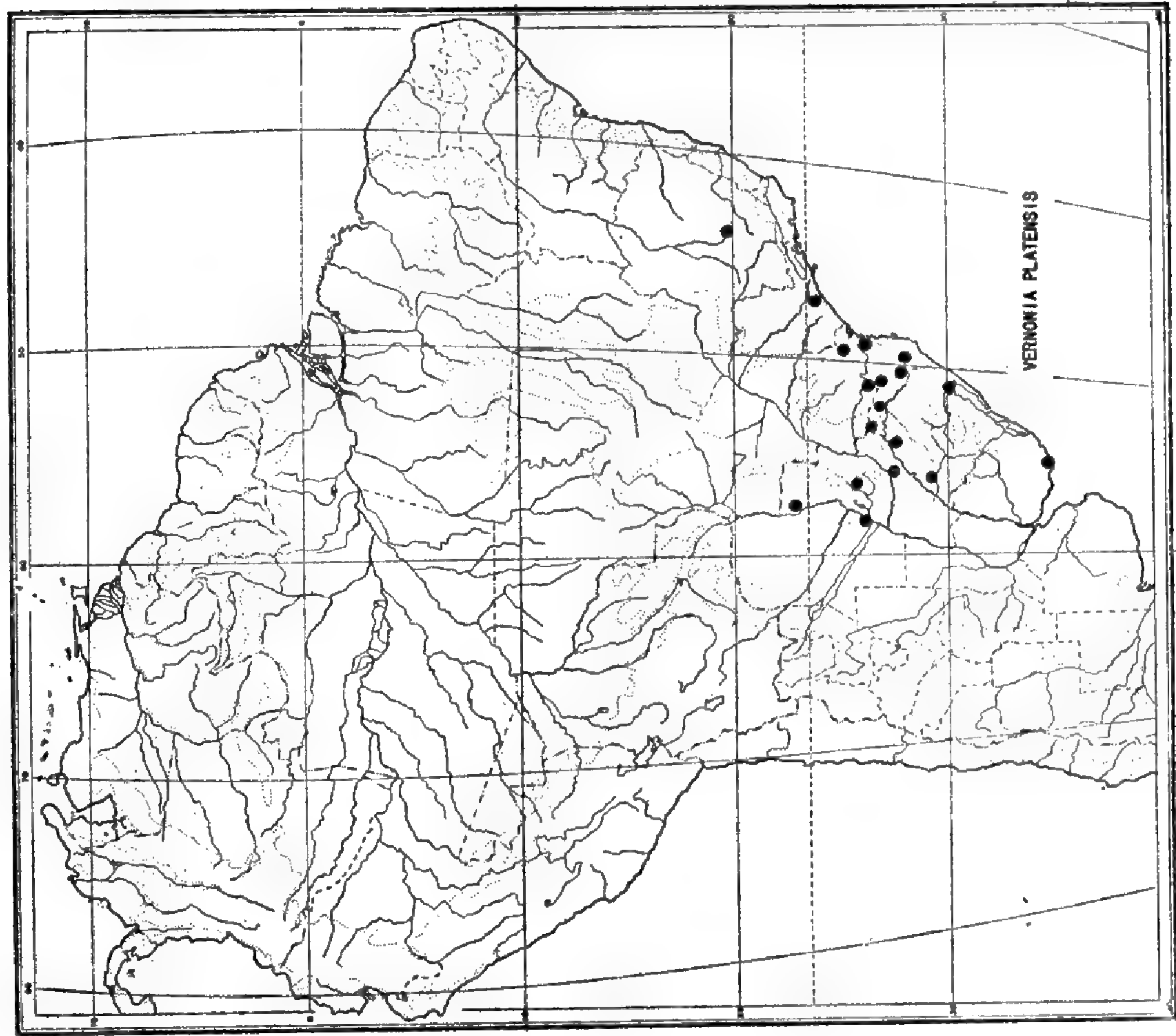
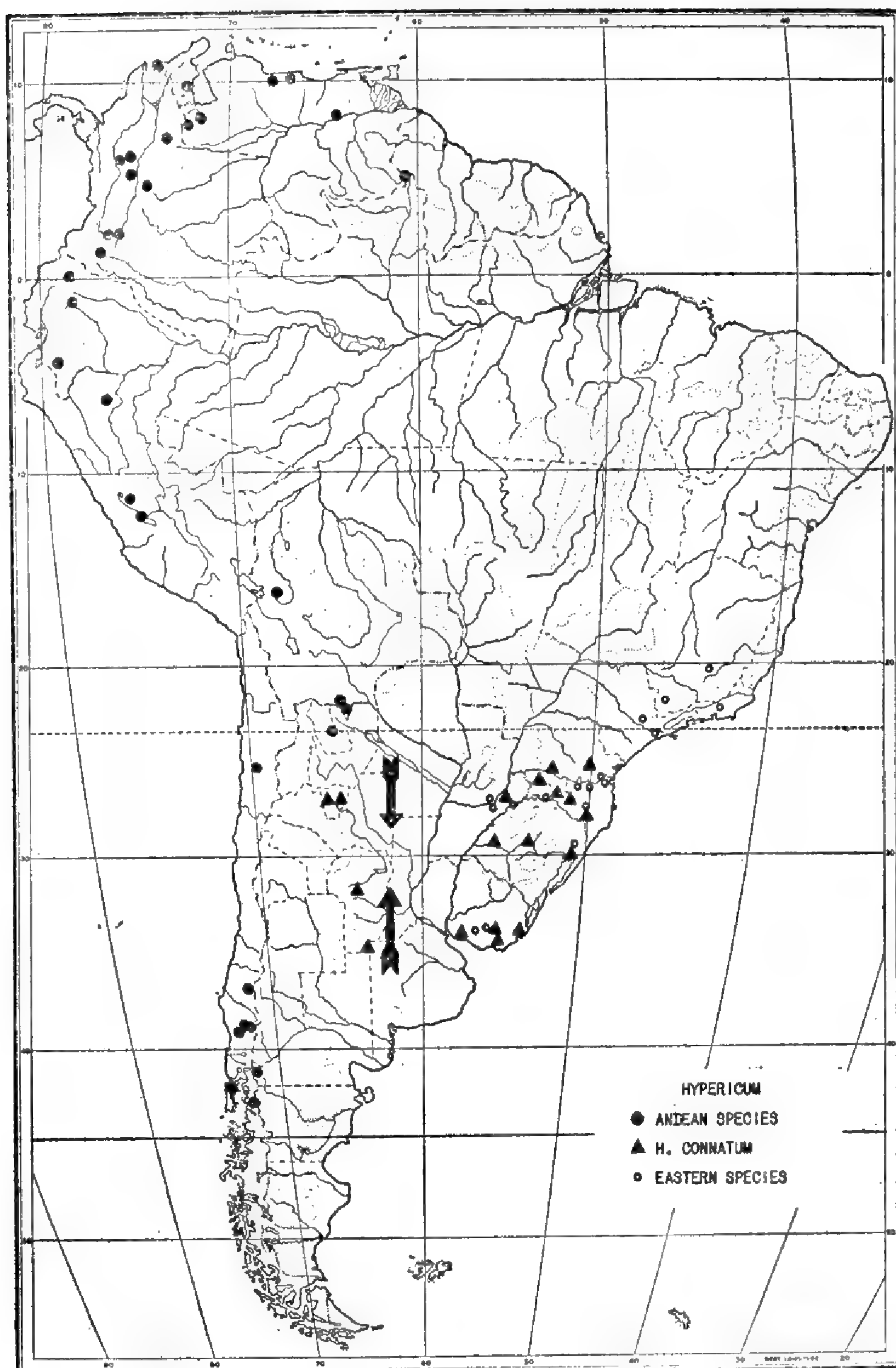
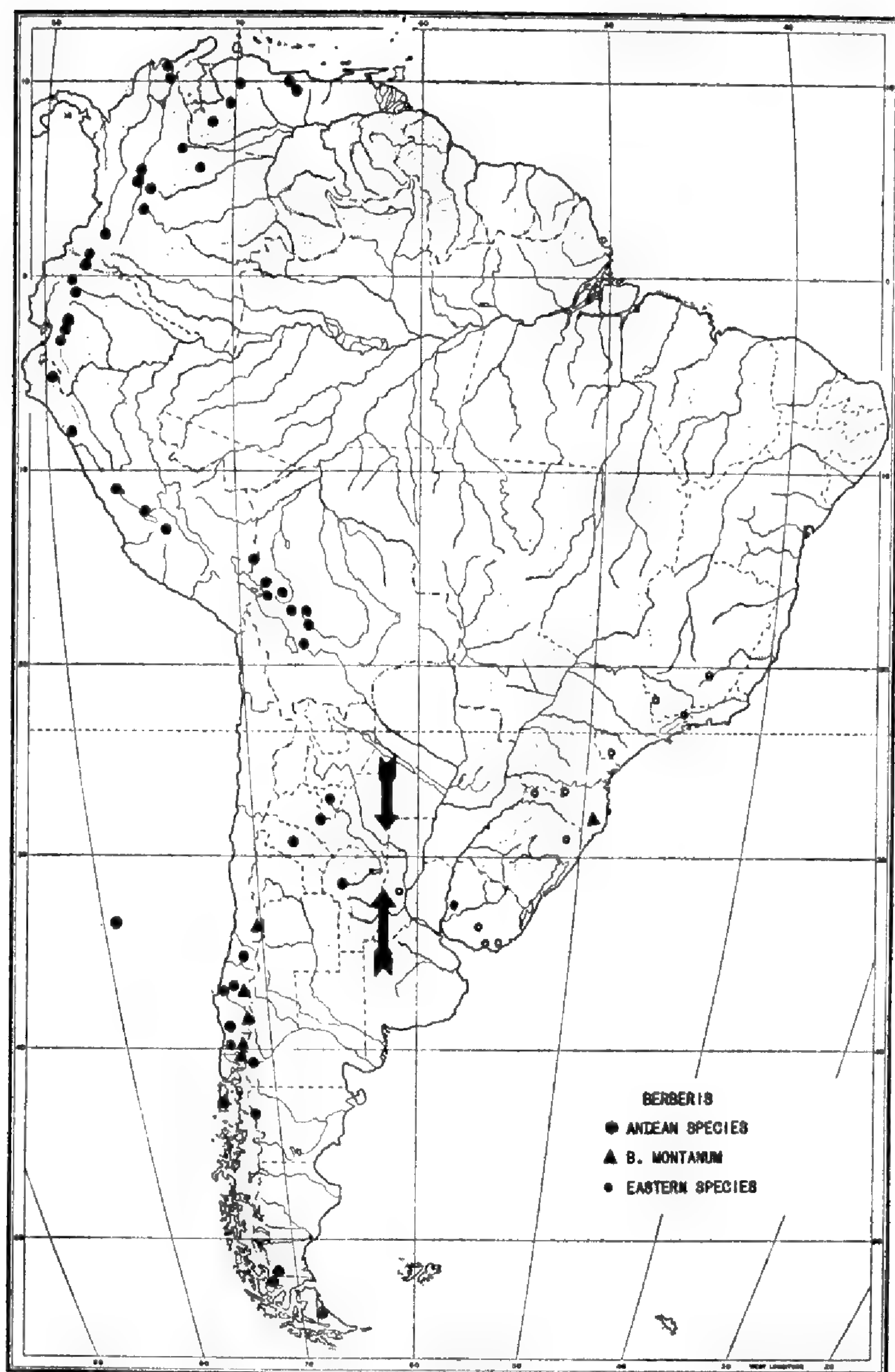


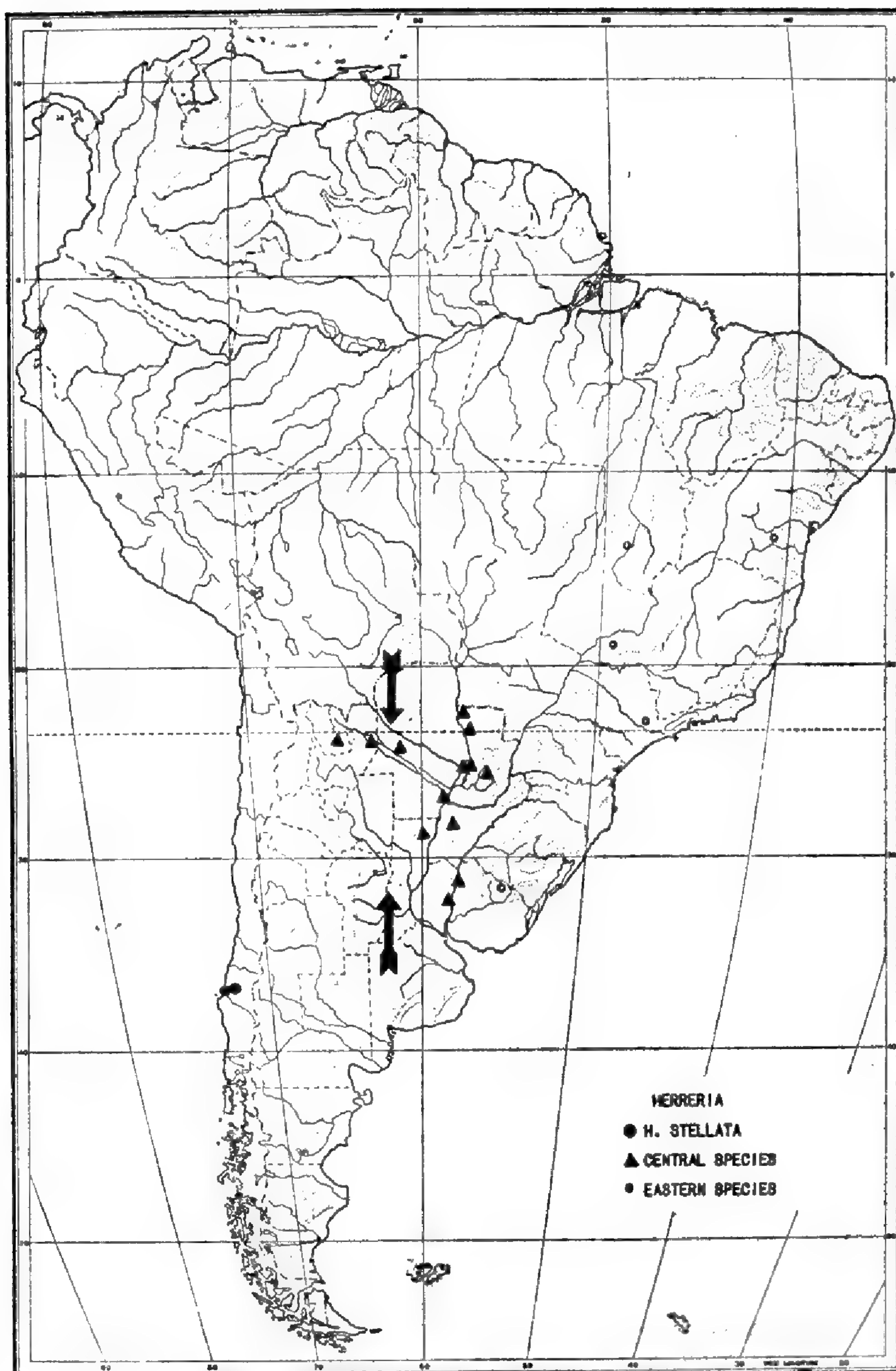
FIGURE 33.—Planalto migration: *Vernonia platensis*.



FIGURE 35.—Climate and topography effecting disjunction of ranges between the Andes and southern Brazil.

FIGURE 36.—Andean migration: *Hypericum*.

FIGURE 37.—Andean migration: *Berberis*.

FIGURE 38.—Andean migration: *Herreria*.

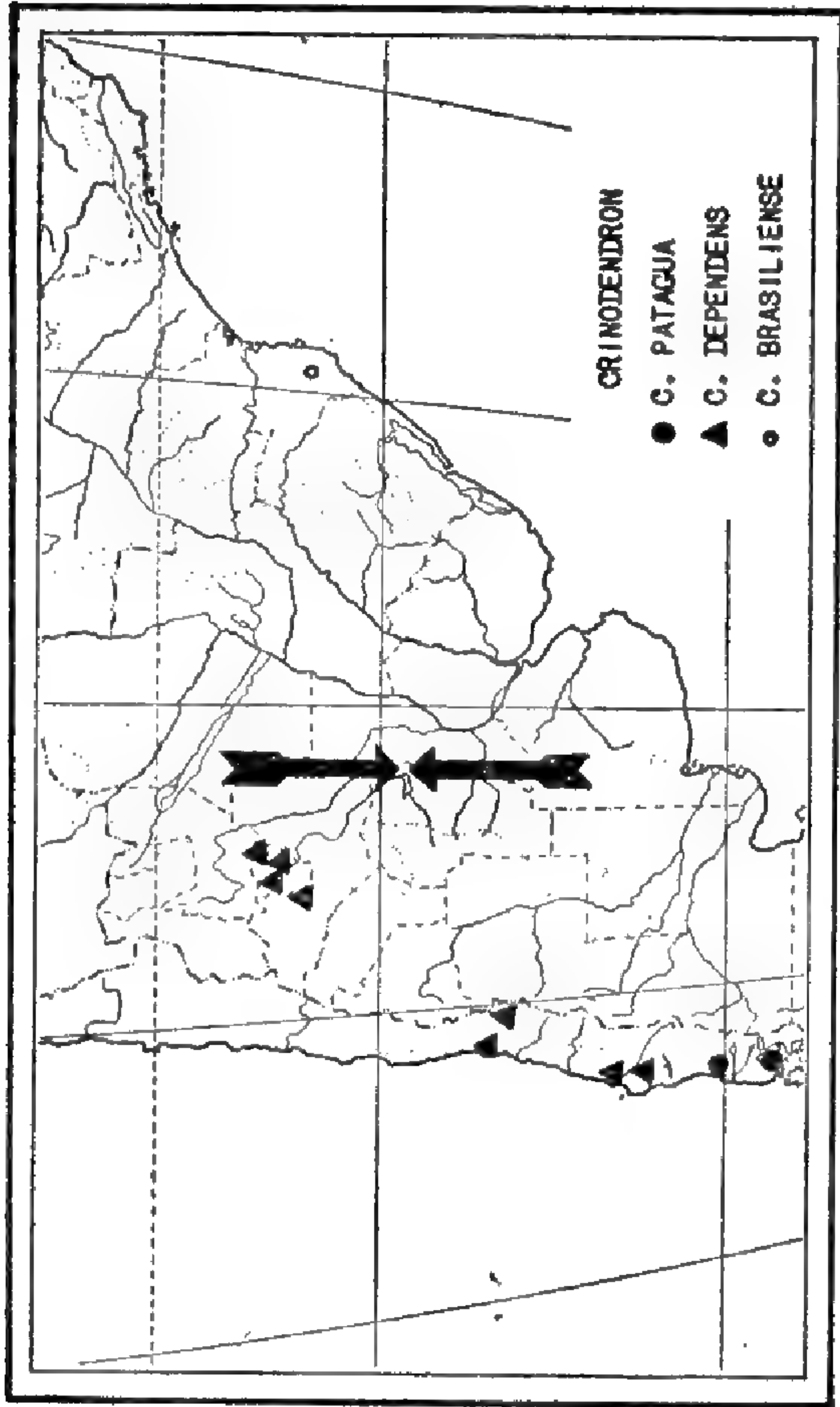


FIGURE 39

FIGURE 40

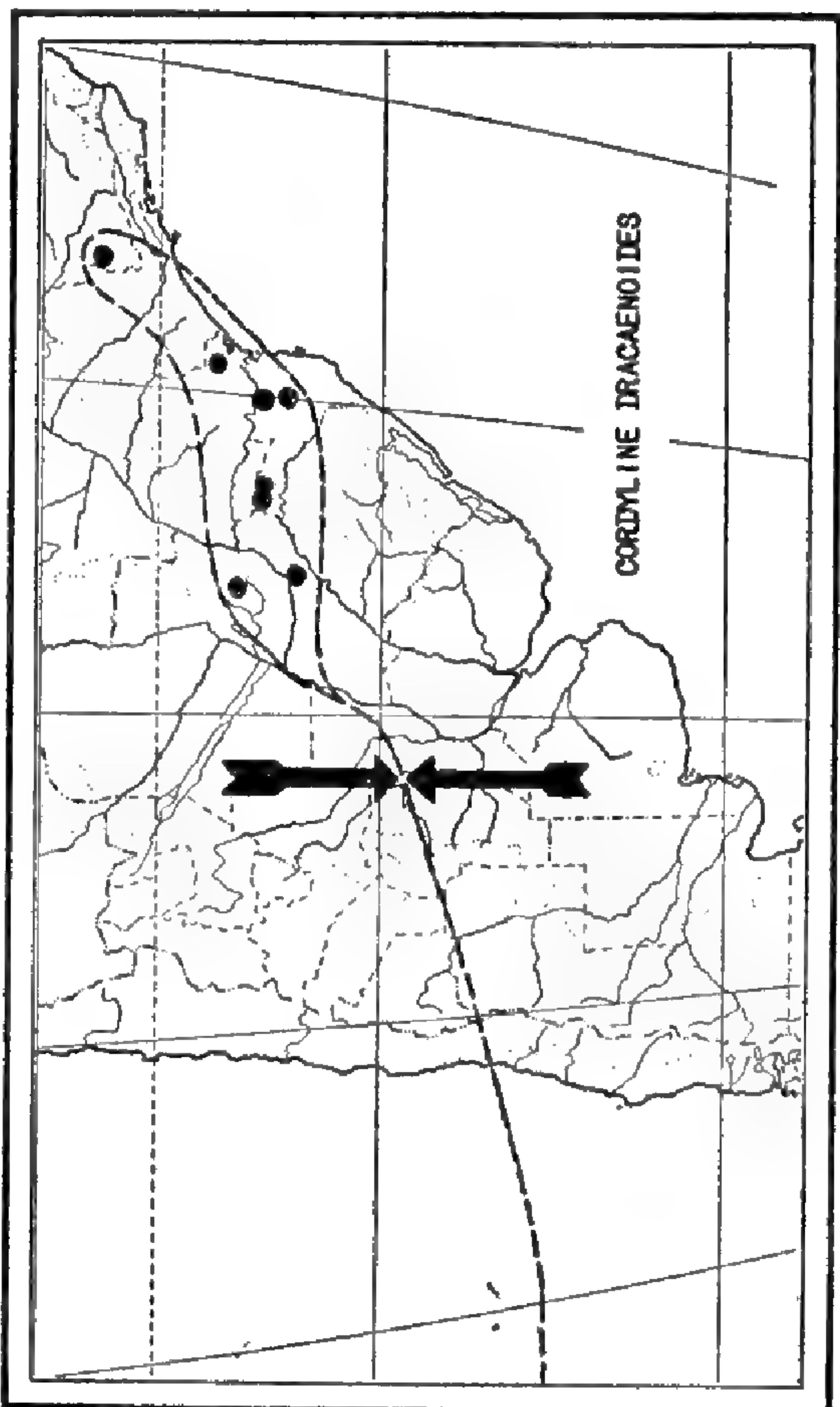


FIGURE 41

FIGURE 42

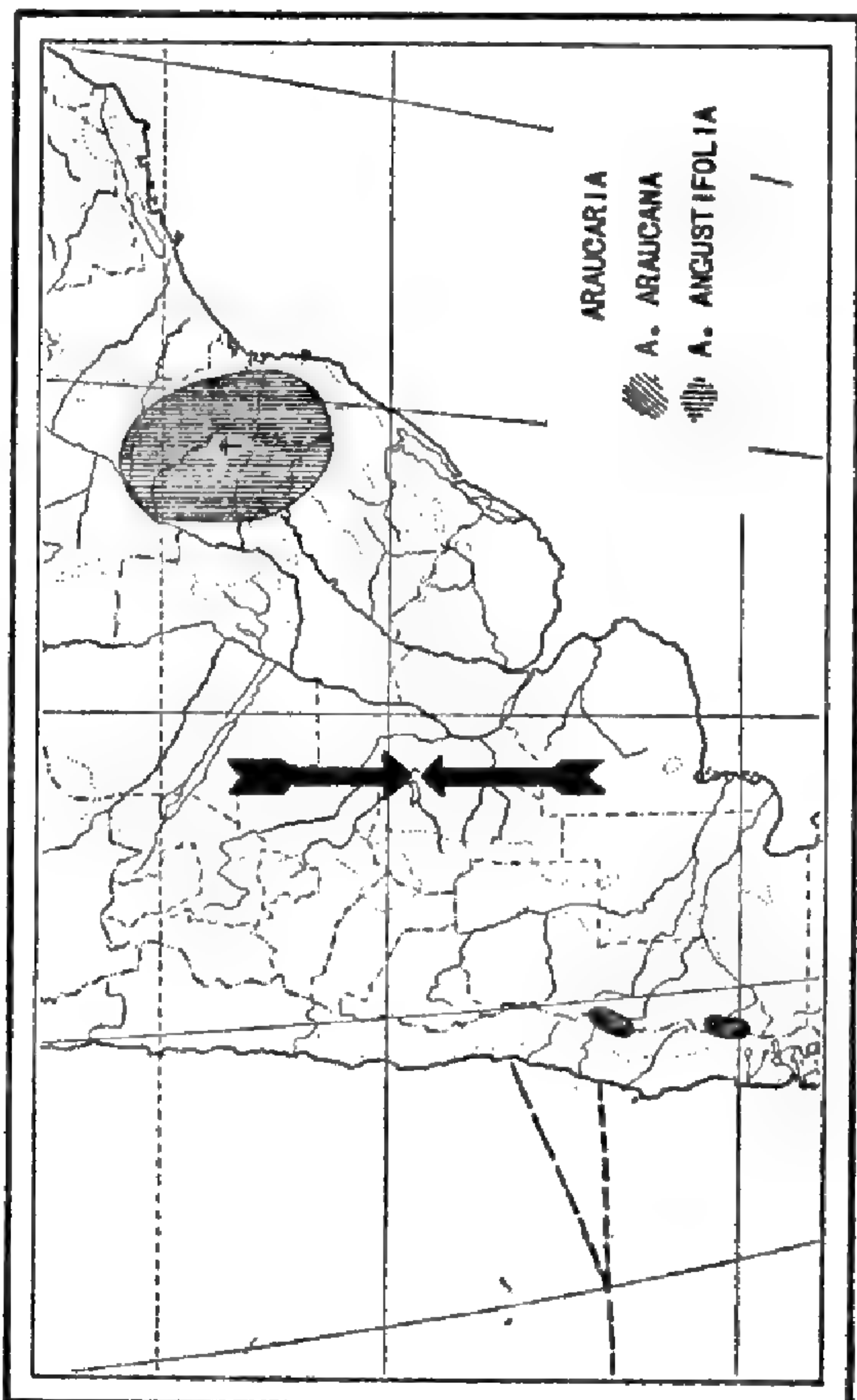
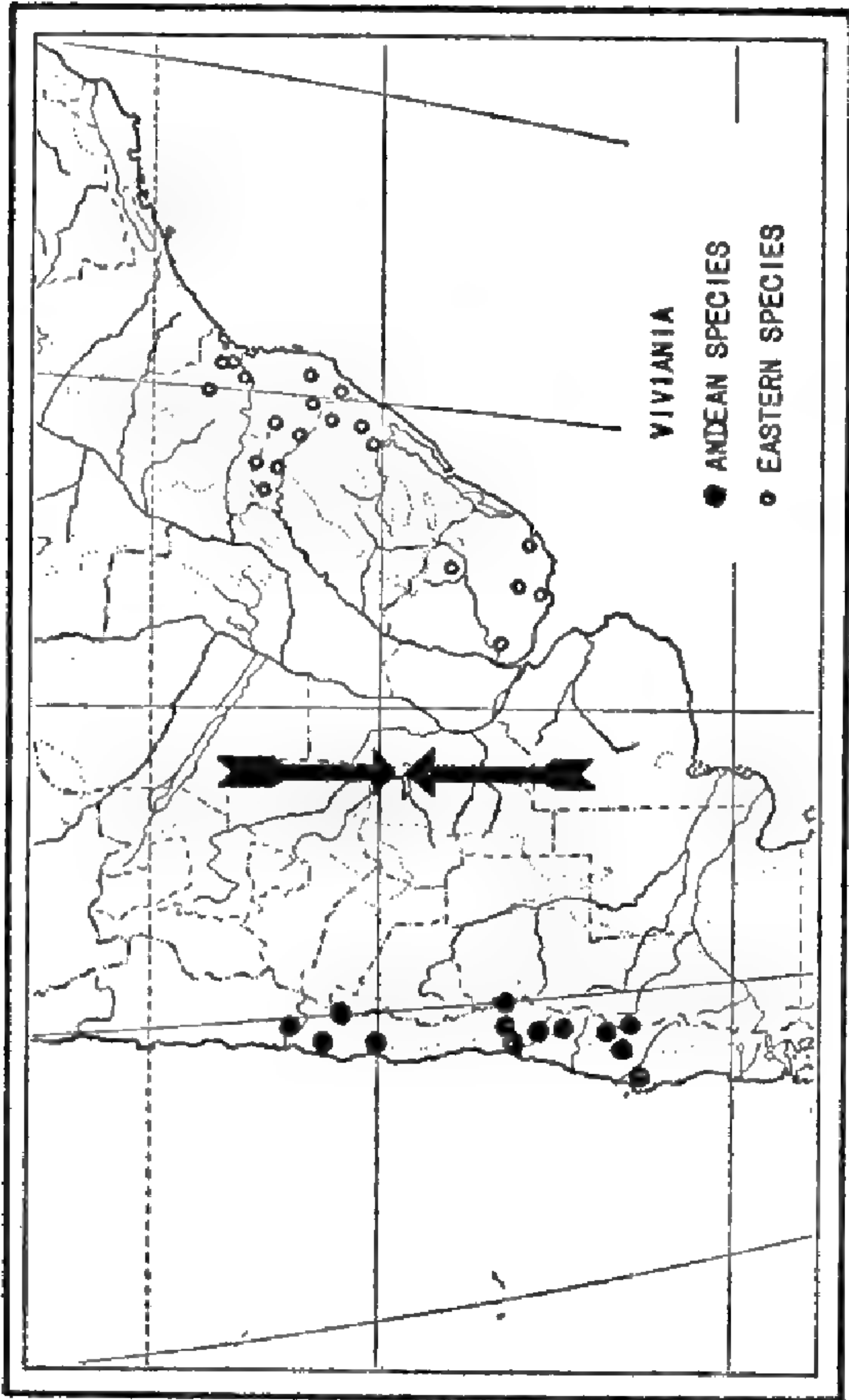


FIGURE 39.—(Top left) Andean migration: *Viviania*.

FIGURE 40.—(Top right) Andean migration: *Crinodendron*.

FIGURE 41.—(Bottom left) Western Pacific migration: *Araucaria*.

FIGURE 42.—(Bottom right) Western Pacific migration: *Cordyline dracaenoides*.

Bibliography

Some of the following works are referred to directly in the text, while others have been used indirectly as background material, but they all add to our information on the subject.

- BACHIGALUPO, NÉLIDA MARÍA. Las especies argentinas de los géneros *Psychotria*, *Palicourea* y *Rudgea* (Rubiaceae). *Darwiniana*, vol. 10, pp. 31–64. 1952.
- BAKER, J. G. Revision of the genera and species of Asparagaceae. *Journ. Linn. Soc.*, vol. 14, pp. 508–632. 1875.
- BARROSO, G. M. Scrophulariaceae indígenas e exóticas no brasil. *Rodriguésia*, vol. 15, No. 27, pp. 9–64. 1952.
- BLACK, GEORGE A. A taxonomic treatment of the genus *Axonopus*. Doctoral thesis, The George Washington University.
- BURKART, ARTURO. Las leguminosas argentinas silvestres y cultivadas, pp. 1–590. 1943.
- CABRERA, ANGEL LULIO. Manual de la flora de los alrededores de Buenos Aires, pp. 1–589. 1953.
- CAIN, STANLEY A. Foundations of plant geography, pp. 1–556. 1944.
- CHODAT, R. La végétation du Paraguay, pp. 1–157. 1916.
- COWAN, R. S. Rutaceae of Santa Catarina. *Sellowia*, No. 12, pp. 79–97. 1960.
- CUATRECASAS, J. A taxonomic revision of the Humiriaceae, *Contr. U.S. Nat. Herb.*, vol. 35, pt. 2, pp. 25–214. 1961.
- DANSEREAU, PIERRE. Biogeography an ecological perspective, pp. 1–394. 1957.
- FERNALD, M. L. Persistence of plants in unglaciated areas of boreal America. *Mem. Amer. Acad. Arts & Sci.*, vol. 15, pp. 295–317. 1925.
- GLEASON, H. A. The progress of botanical exploration in tropical South America. *Bull. Torrey Bot. Club*, vol. 59, pp. 21–28. 1932.
- HAUMAN, L., BURKART, A., PARODI, L. R., & CABRERA, A. L. La Vegetación de la Argentina, pp. 1–349. 1947.
- HOEHNE, F. C. Phytophysionomia do estado do Matto-Grosso (with map), pp. 1–104. 1923.
- . Indice bibliográfico e numérico das plantas colhidas pela Comissão Rondon, pp. 1–400. 1951.
- KLEIN, R. M. O aspeto dinâmico do pinheiro brasileiro. *Sellowia*, No. 12, pp. 17–44. 1960.
- KNUTH, R. Geraniaceae. *Engler, Pflanzenreich*, iv. Fam. 129, pp. 1–640. 1912.
- LAWRENCE, GEORGE H. M. Taxonomy of Vascular Plants, pp. 1–823. 1951.
- MARTIUS, K. F. P. VON. *Flora Brasiliensis*, 15 vols. 1804–1906.
- MOLDENKE, H. N. A résumé of the Verbenaceae, Avicenniaceae, Stilbaceae, Symphoremaceae and Eriocaulaceae of the world as to valid taxa, geographic distribution and synonymy, pp. 1–495. 1959a.
- . Supplement I, pp. 1–26. 1959b.
- . Supplement II, pp. 1–16. 1960.
- PIRES, J. MURÇA. Monografia Quiinaceae, ined.

- RADLKOFER, L. Sapindaceae. Engler, Pflanzenreich, iv. Fam. 165, pp. 1-1539. 1931-34.
- RAMBO, BALDUINO. A imigração da selva higrófila no Rio Grande do Sul. Sellowia, No. 3, pp. 55-91. 1952.
- . Der Regenwald am oberen Uruguay. Sellowia, No. 7, pp. 183-233. 1956a.
- . A flora fanerogamica dos aparados Riograndenses. Sellowia, No. 7, pp. 235-298. 1956b.
- . A fisionomia do Rio Grande do Sul. Jesuitas no sul do Brasil, ed. 2, vol. 6, pp. 1-456. 1956c.
- . Die Europäischen Unkräuter in Südbrasilien. Sellowia, No. 12, pp. 45-78. 1960.
- REITZ, RAULINO. As palmeiras de Santa Catarina e a sua distribuição geográfica. An. Bot. Herb. "Barbosa Rodrigues," No. 5, pp. 233-252. 1953.
- . As Halorrhagaceae de Santa Catarina. Sellowia, No. 6, pp. 237-242. 1954.
- . Aráceas catarinenses. Sellowia, No. 8, pp. 20-70. 1957.
- REITZ, RAULINO, AND SMITH, LYMAN B. Crinodendron no Brasil. Sellowia, No. 9, pp. 19-21. 1958.
- RICHARDS, P. W. The tropical rain forest, an ecological study, pp. 1-450. 1952.
- ROJAS, TEODORO, AND CARABIA, J. P. Breve reseña de la vegetación Paraguaya. In Verdoorn, Plants and plant science in Latin America, pp. 121-125. 1945.
- SAMPAIO, A. J. DE. Phytogeographia do Brasil, ed. 3, pp. 1-372. 1945.
- SCHNEIDER, C. K. Die Gattung Berberis (Euberberis), Vorarbeiten für eine Monographia. Bull. Herb. Boiss. II. vol. 5, pp. 33-48, 133-148, 391-403, 449-464, 655-670, 800-831. 1904-05.
- SCOGGAN, H. J. The flora of Bic and the Gaspé Peninsula, Quebec. Nat. Mus. Canada, Bull. 115, pp. 1-399. 1950.
- SLEUMER, H. Estudios sobre el genero "Dunalia" H. B. K. Lilloa, vol. 23, pp. 117-142. 1950.
- SMITH, A. C., & JOHNSTON, I. M. A phytogeographic sketch of Latin America. In Verdoorn, Plants and plant science in Latin America, pp. 11-18. 1945.
- SMITH, LYMAN B. Geographical evidence on the lines of evolution in the Bromeliaceae. Bot. Jahrb., vol. 66, pp. 446-468. 1934.
- . Studies in the Bromeliaceae—VI. Proc. American Acad. Sci., vol. 70, pp. 147-220. 1935.
- . The vegetation of Brazil. In Verdoorn, Plants and plant science in Latin America, pp. 297-302. 1945.
- . The Bromeliaceae of Brazil. Smithsonian Misc. Coll., vol. 126, pp. 1-290. 1955.
- . Notes on South American phanerogams—I. Journ. Washington Acad. Sci., vol. 9, pp. 282-284. 1958a.
- . Notes on South American phanerogams—II. Journ. Washington Acad. Sci., vol. 48, pp. 310-314. 1958b.
- SMITH, LYMAN B., AND DOWNS, ROBERT J. Resumo preliminar das Rubiáceas de Santa Catarina. Sellowia, No. 7, pp. 13-86. 1956.
- . Resumo preliminar das Euforbiáceas de Santa Catarina. Sellowia, No. 11, pp. 155-231. 1959.
- . Resumo preliminar das Amarantáceas de Santa Catarina. Sellowia, No. 12, pp. 99-120. 1960a.
- . Resumo preliminar das Cariofiláceas de Santa Catarina. Sellowia, No. 12, pp. 121-133. 1960b.
- . The Xyridaceae of Brazil. (In preparation.)

- STAFLEU, F. A. A monograph of the Vochysiaceae, I. Salvertia and Vochysia. Rec. Trav. Bot. Néerl., vol. 41, pp. 397–540. 1948.
- SWART, J. J. A monograph of the genus *Protium* and some allied genera (Burseraceae). Rec. Trav. Bot. Néerl., vol. 39, pp. 211–446. 1942.
- WULFF, E. V. Introduction to the historical geography of plants. Bull. Appl. Bot. Gen. & Pl. Breeding. Suppl. 52. (translation Brissenden, E.): An introduction to historical plant geography. pp. 1–223. 1943.

PART 4

A SYNOPSIS OF THE AMERICAN VELLOZIACEAE

LYMAN B. SMITH

Introduction

The present paper is a necessary corollary to my research on the origin of the flora of southern Brazil that was supported by a grant from the National Science Foundation in 1956–57. Although none of my 1956–57 collections are represented here, the Velloziaceae are one of the best examples of the distribution of a family of consistently heliophile species, and its extension southward from the planalto of central Brazil provides a pattern to illustrate the movement of many other groups.

The American species of Velloziaceae have not been organized since Seubert's treatment in the "Flora Brasiliensis" in 1847 and then only sketchily and without complete keys. In 1937, Goethart and Henrard published many new species without any key whatever, but this has only aggravated the problem of classifying new material. Thus, in order to make the material available for phytogeographic studies it is first necessary to revise it. A number of American herbaria have been consulted and photographs of most of the types of Goethart and Henrard have been obtained from the Berlin-Dahlem herbarium through the kindness of Dr. G. M. Schulze and of Frau Christa Metzger, who had them on loan from Leiden. Frau Metzger is working on material in European herbaria with special emphasis on leaf anatomy. The present paper was begun without knowledge of her work, but since all novelties are based on material in American herbaria it should prove largely supplementary.

In preparing the present paper, I am indebted to the curators of the following herbaria for the opportunity to study the material in their care:

Chicago Natural History Museum (F)
Gray Herbarium of Harvard University (GH)
Instituto Agronômico do Norte (IAN)
Museu Paraense "Emilio Goeldi" (MG)
New York Botanical Garden (NY)
University of California (UC)
United States National Herbarium (US)

Exsiccatae have been cited only for novelties and new combinations, but many that do not appear have been most helpful in making keys and studying distribution. My knowledge of the older species has been much increased by the type photographs of J. Francis Macbride received from the Chicago Natural History Museum, and N. Y. Sandwith has kindly communicated locality data of Gardner's collections from his notebook at Kew.

Some of the earliest authors to treat the Velloziaceae, like Kunth, confused the group with the Bromeliaceae, presumably on the basis of habital resemblances. However, it is clear from the character of the endosperm as well as of the perianth that the Velloziaceae are much more closely allied to the Amaryllidaceae. In fact, under the broad interpretation of the Amaryllidaceae, Baker was doubtless more logical to include the Velloziaceae as a tribe, Vellozieae, than was Pax to maintain it as a separate family. In a system such as Hutchinson's, the Velloziaceae, as distinguished by stalked placentas and many-ranked ovules, are reasonably equivalent to the new units derived from the division of the Liliaceae and Amaryllidaceae.

The primary subdivision of the Velloziaceae has been based on three different sets of characters according to the authors involved. Baker and Hutchinson used the presence or absence of an extension of the perianth-tube above the ovary. This is a distinction which is striking between extremes but which is so finely intergrading from species to species in a complete survey that it is quite unworkable. Pax used the distinction between 6 stamens and more than 6, and since no species combining the two has yet been found, his system can be said to be workable. However, it places under *Barbacenia* species that are in every other respect indistinguishable from *Vellozia*, and furthermore it is quite illogical because species with 9 stamens have some tepals subtending a single stamen as in *Barbacenia* and others subtending more than one as in *Vellozia*. Seubert used the form of the filament, which is a clear and logical distinction with good correlations. For instance, sharp cleavage of leaf-blades and broad 3-lobed stigmas are restricted to *Vellozia* by Seubert's classification. It is difficult to understand how later authors could have overlooked or disregarded his system.

Velloziaceae

Drude *in* Schenck, Handb. Bot. 333. 1886; Pax *in* Engl. & Prantl, Pflanzenfam. 2, Abt. 5: 125. 1887; ed. 2. 15a: 431. 1930; Hutchinson, Fam. Fl. Pl. ed. 2. 2: 678. 1959.

Amaryllideae-Vellozieae D. Don, Edinb. New Philos. Journ. 8: 164. 1830; Baker *in* Benth. & Hook. Gen. Pl. 3: 739. 1880.

Family *Vellozieae* Seubert *in* Mart. Fl. Bras. 3, pt. 1: 65. 1847.

Perennial plants; indument highly diverse, often not strictly epidermal (Greves, Journ. Bot. 59:274. 1921); stems (caudex) woody, fibrous, simple or dichotomously branched, covered with persistent leaf-sheaths; complete leaves clustered at the end of the stem or its branches, grass-like; scapes one or more, terminal becoming lateral by the elongation of the axis; flowers solitary on each peduncle, perfect, actinomorphic, brightly colored; perianth-tube equaling to greatly exceeding the ovary and adnate to it; tepals in 2 series but mostly very similar, erect to reflexed at anthesis; stamens 6 to numerous in 6 bundles; filaments terete and simple or flat with 2 lobes or appendages at the summit, rarely lacking; anthers basifixed to medifixed, opening by longitudinal slits; ovary 3-locular, inferior; style slender but usually enlarged by the stigmas; ovules numerous in many rows on stalked placentas; fruit a capsule; seeds numerous; embryo small; endosperm copious, non-farinaceous.

1. Anthers basifixed; stigma broadly 3-lobed; leaf-blades deciduous along a straight transverse line; stamens 6 or usually more, the filaments terete and elongate, unappendaged above **1. Vellozia**

1. Anthers dorsifixed, although sometimes only slightly above the base; stigma slightly if at all lobed; leaf-blades tardily and irregularly deciduous; stamens always 6.

2. Filaments very short, terete, unappendaged, the anthers appearing sessile.

2. Barbaceniopsis

2. Filaments evident, flat with two lobes or appendages at the summit.

3. Barbacenia

1. Vellozia

Vellozia Vand. Fl. Lusit. & Brasil. Spec. 32, pl. 2. 1788.

Xerophyta Juss. Gen. 50. 1789.

Campteria A. Rich. Bull. Soc. Philom. 79. 1822.

Radia A. Rich. in Kunth, Syn. Pl. Aequin. 1: 300. 1822.

Schnizleinia Steud. ex Hochstetter in Flora 27: 31. 1844.

Talbotia Balf. in Trans. Bot. Soc. Edinb. 9: 190. 1868.

Plants from small stature to over 4 meters high; caudex mostly few-many-branched; leaf-blades deciduous along a straight transverse line; tepals free above the ovary or forming a tube; stamens 6, or more numerous and in 6 bundles; filaments terete and filamentous.

Type species: *Vellozia glabra* Mikan.

Keys to the Species of Vellozia

1. Tepals free or obscurely short-connate above the ovary . . . Section I. **Vellozia**

1. Tepals forming a distinct tube above the ovary . . . Section II. **Radia**

SECTION I. VELLOZIA

1. Ovary (or capsule) smooth and glabrous.

2. Plant nearly stemless; leaves 5–7 cm. long.

3. Stamens subequal; phalanges simple **1. V. macedonis**

3. Stamens very unequal; phalanges appendaged **2. V. tenella**

2. Plant distinctly caulescent.
 4. Scapes less than 1 cm. long; capsule obconic or truncate.
 5. Stamens 6; leaf-blades obtuse or acute.
 6. Leaf-blades acute, ciliate; sheaths pubescent . . . 3. *V. abietina*
 6. Leaf-blades obtuse, serrulate 4. *V. tragacantha*
 5. Stamens more than 6; leaf-blades retuse 5. *V. pusilla*
 4. Scapes much more than 1 cm. long.
 7. Caudex simple or subsimple; leaf-blades only 2.5 cm. long.
 6. *V. sellovii*
 7. Caudex branched; leaf-blades at least 8 cm. long.
 8. Stamens 6; leaf-blades lanceolate, widest at the middle.
 7. *V. plicata*
 8. Stamens more than 6; leaf-blades linear or very narrowly triangular.
 9. Capsule alate-trigonous, broadest at the middle, dull; leaf-blades filiform-acuminate, coarsely brown-ciliate near the base.
 8. *V. alata*
 9. Capsule terete to trigonous but not alate, broadest at apex, lustrous.
 10. Scapes erect; leaves filiform-acuminate. 9. *V. glabra*
 10. Scapes recurved; leaves broadly acute to retuse.
 10. *V. incurvata*
 1. Ovary (or capsule) at least partially vestite.
 11. The ovary vestite primarily on the angles or base.
 12. Trichomes of the ovary acute, making the angles scabrous, concolorous with the ovary.
 13. Tepals 60–70 mm. long; leaf-blades obtuse to subacute; old leaf-sheaths mostly entire 11. *V. compacta*
 13. Tepals 30 mm. long.
 14. Old leaf-sheaths mostly entire; leaf-blades acuminate (?).
 12. *V. verruculosa*
 14. Old leaf-sheaths splitting into coarse fibers; leaf-blades obtuse to subacute 13. *V. fibrosa*
 12. Trichomes of the ovary rounded, glandular in character.
 15. Leaf-blades acuminate; tepals 40–60 mm. long . . . 14. *V. variabilis*
 15. Leaf-blades subacute to retuse.
 16. Glands of the ovary stipitate; leaf-sheaths splitting into fibers.
 17. Fibers of the leaf-sheaths straight (?) 15. *V. ambigua*
 17. Fibers of the leaf-sheaths incurved 16. *V. martiana*
 16. Glands of the ovary sessile.
 18. Tepals obtuse and submucronulate; leaf-blades 9–15 mm. wide.
 17. *V. wettsteinii*
 18. Tepals acute; leaf-blades not more than 3 mm. wide.
 19. Leaf-blades to 18 cm. long, 3 mm. wide . . . 18. *V. angustifolia*
 19. Leaf-blades less than 4 cm. long; about 1 mm. wide.
 19. *V. virgata*
 11. The ovary completely vestite or laxly and evenly vestite.
 20. Indument of the ovary glandular in character.
 21. Leaves acuminate or subulate-acuminate.
 22. Capsule oblong.
 23. Leaf-blades narrow, not over 6 mm. wide; bases of the glands stout, confluent 20. *V. echinata*

- 23. Leaf-blades 10 mm. or broader.
 - 24. Margins of the leaf-blades pilose; stamens 15.
 - 21. V. fimbriata**
 - 24. Margins of the leaf-blades merely scabrous; stamens 30–36.
 - 22. V. intermedia**
- 22. Capsule (or ovary) ovoid, globose, or hemispheric.
 - 25. Ovary broad at apex, hemispheric or broadly truncate.
 - 26. Margins of the leaf-blades pilose; stamens 30.
 - 23. V. barbaceniifolia**
 - 26. Margins of the leaf-blades serrulate; stamens 18.
 - 24. V. hemisphaerica**
 - 25. Ovary contracted at apex, ovoid, or globose.
 - 27. Scape less than 2 cm. long; tepals obovate, rounded, 50 mm. long **25. V. breviscapa**
 - 27. Scape elongate.
 - 28. Leaf-blades about 3 mm. wide; caudex slender with few ranked laxly imbricate leaf-sheaths. **26. V. squalida**
 - 28. Leaf-blades 15 mm. or broader; caudex stout with many-ranked very densely imbricate leaf-sheaths.
 - 29. Tepals 75 mm. long; leaf-blades pubescent beneath; ovary densely glandular-hirsute **27. V. aloifolia**
 - 29. Tepals 45 mm. long; leaf-blades glabrous; ovary subdensely and coarsely stipitate-glandular **28. V. viannae**
- 21. Leaves broadly subacute, obtuse or emarginate.
 - 30. Margins of the leaf-blades entire and glabrous.
 - 31. Ovary rufescent-pilose; leaf-blades gray villous beneath.
 - 29. V. glandulifera**
 - 31. Ovary scabrous-glandular; leaf-blades very glutinous.
 - 30. V. scoparia**
 - 30. Margins of the leaf-blades serrate, setose, or pilose.
 - 32. Leaf-blades wholly white-pilose, 1.5 mm. wide, ecarinate.
 - 31. V. pilosa**
 - 32. Leaf-blades incompletely vestite if at all.
 - 33. Glands of the ovary sessile or subsessile; capsule widest near the apex.
 - 34. Stamens 6; peduncle less than 1 cm. long . . . **32. V. taxifolia**
 - 34. Stamens 18–30; peduncle much longer than 1 cm.
 - 35. Tepals 2 cm. long; stamens 18 **33. V. declinans**
 - 35. Tepals 4 cm. long; stamens 30 (?) **16. V. martiana**
- 33. Glands of the ovary stipitate.
 - 36. Sheaths ciliate throughout with stiff spreading setae.
 - 34. V. barbata**
 - 36. Sheaths entire or with a few teeth toward apex.
 - 37. Capsules trigonous or oblong.
 - 38. Sheaths aculeolate toward apex; capsules trigonous, 12-costate; tepals linear-lanceolate, acute.
 - 35. V. pleurocarpa**
 - 38. Sheaths entire; capsules oblong; tepals linear-spathulate.
 - 36. V. leptopetala**
 - 37. Capsules ellipsoid or globose.
 - 39. Leaf-sheaths densely white-lanate at apex; blades subdensely setose beneath; tepals 40–50 mm. long.
 - 37. V. resinosa**

- 39. Leaf-sheaths glabrous; tepals smaller.
- 40. Sheaths wholly covered; caudex very short and stout. **38. V. brevifolia**
- 40. Sheaths much exposed toward their apices; caudex slender.
- 41. Plants of medium stature, well over 25 cm. high; leaf-blades serrulate **39. V. epidendroides**
- 41. Plants dwarfed, less than 25 cm. high.
- 42. Leaf-blades straight, 1 mm. wide, laxly vestite with dark sessile glands **40. V. minima**
- 42. Leaf-blades contorted, 3 mm. wide, subdensely setose **41. V. streptophylla**
- 20. Indument of the ovary punctulate, acute, or sharply truncate, not glandular in character.
- 43. Trichomes of the ovary minute, making it scabrous or granulate and generally exposing its surface in between.
- 44. Scape none; capsule hidden in the leaf-sheaths, obconic.
- 45. Leaf-blades 2.5 cm. long, emarginate **32. V. taxifolia**
- 45. Leaf-blades 9-10 cm. long, subobtusate **42. V. cryptantha**
- 44. Scape evident.
- 46. Ovary ovoid or ovoid-globose.
- 47. Caudex to 2 meters high, much branched; leaf-blades deeply retuse, 5 mm. wide; old sheaths not splitting into fibers. **43. V. ramosissima**
- 47. Caudex not over 20 cm. high, simple or few-branched.
- 48. Leaf-blades obtuse; old sheaths densely imbricate, splitting; caudex very short **44. V. asperula**
- 48. Leaf-blades retuse; old sheaths much exerted, entire; caudex to 20 cm. high **36. V. leptopetala**
- 46. Ovary oblong or oblong-ellipsoid.
- 49. Tepals 40-50 mm. long.
- 50. Scape nearly glabrous; tepals long-attenuate toward base, white (?) **45. V. punctulata**
- 50. Scape strongly vestite on the upper half; tepals lanceolate, blue **46. V. bradei**
- 49. Tepals 10-20 mm. long.
- 51. Margins of the blades entire; sheaths remaining entire; blades 12 mm. wide, glaucous beneath . . **47. V. piresiana**
- 51. Margins of the blades serrulate; sheaths splitting into coiled fibers.
- 52. Leaf-blades 3-4 mm. wide; tepals 20 mm. long. **48. V. ornata**
- 52. Leaf-blades to 7 mm. wide; tepals 10 mm. long. **49. V. granulata**
- 43. Trichomes of the ovary coarse, completely covering it.
- 53. Leaf-blades acuminate or subulate-acuminate.
- 54. Scape glabrous or at most slightly scabrous at apex, contrasting sharply with the densely vestite ovary.
- 55. Trichomes of the ovary broadly truncate with contiguous apices **50. V. flavicans**

55. Trichomes acute or obtuse and laterally flattened but not truncate.
56. Trichomes of the ovary short, ovoid; leaf-sheaths entire. **51. *V. glauca***
56. Trichomes of the ovary elongate, subulate or laterally flattened.
57. Leaf-sheaths remaining entire.
58. Blades strongly sulcate **52. *V. glochidea***
58. Blades nearly even **53. *V. gardneri***
57. Leaf-sheaths splitting into fibers.
59. Ovary-trichomes subulate, acute; leaf-blades glabrous beneath except the keel **54. *V. crassicaulis***
59. Ovary-trichomes much flattened laterally, obtuse; leaf-blades villous beneath **55. *V. sulphurea***
54. Scape strongly vestite on the upper third or half, not contrasting with the ovary.
60. Leaf-blades 15 mm. wide; tepals 80–120 mm. long; scape muricate toward apex.
61. Scape 7 cm. long; ovary-trichomes abruptly attenuate. **56. *V. seubertiana***
61. Scape to 40 cm. long; ovary trichomes sharply truncate. **57. *V. froesii***
60. Leaf-blades 4–8 mm. wide (uncertain in *V. pumila*); scape 2–4.5 cm. long above the leaf-sheaths.
62. Tepals 20 mm. long **58. *V. hypoxoides***
62. Tepals 40–80 mm. long.
63. Sheaths splitting into fibers.
64. Caudex ovoid, 4 cm. long; leaf-margins and keel subdensely aculeolate; tepals 40 mm. long. **59. *V. pumila***
64. Caudex cylindric, elongate; leaf-margins and keel entire and glabrous; tepals 80 mm. long . . . **60. *V. swallenii***
63. Sheaths remaining entire; plant stemless; tepals 60 mm. long. **61. *V. bulbosa***
53. Leaf-blades broadly subacute, obtuse, or emarginate.
65. Scape glabrous, contrasting sharply with the densely vestite ovary.
66. Leaf-sheaths remaining entire; ovary subglobose. **62. *V. cinerascens***
66. Leaf-sheaths splitting into coarse fibers; ovary clavate-cylindric, truncate **63. *V. circinans***
65. Scape strongly vestite toward apex.
67. Trichomes of scape and ovary fine, filamentous. **64. *V. dasypus***
67. Trichomes of scape and ovary much coarser.
68. Ovary prismatic, its trichomes subulate, more or less twisted **65. *V. glaziovii***
68. Ovary terete or if trigonous, broader at center, base, or apex.
69. Plant essentially stemless.
70. Leaf-blades ciliate-serrate **66. *V. crinita***
70. Leaf-blades merely serrate; ovary acutely trigonous. **67. *V. caruncularis***

- 69. Plant long-caulescent.
 - 71. Scape about equaling the leaves, ca. 13 cm. long.

68. *V. gracilis*
 - 71. Scape much exceeded by the leaves.
 - 72. The scape trigonous; ovary-trichomes in part bicuspidate 69. *V. grisea*
 - 72. The scape terete; ovary-trichomes acute.

70. *V. exilis*

SECTION II. RADIA

- 1. Scapes not over 3 cm. long.
 - 2. Tepals 2 cm. long; leaf-blades 3–5 cm. long; flowers numerous, sessile.

71. *V. uaipanensis*
 - 2. Tepals 8 cm. or longer; leaf-blades to 27 cm. long; flowers solitary.
 - 3. Flowers sessile 72. *V. markgrafii*
 - 3. Flowers scapose.
 - 4. Leaf-blades subappressed-pilose beneath, 4 mm. wide . 73. *V. riedeliana*
 - 4. Leaf-blades glabrous except for the ciliate keel and margins, 10 mm. wide 74. *V. maguirei*
- 1. Scapes elongate.
 - 5. Perianth-tube not more than 30 mm. long above the ovary.
 - 6. Scape 6–15 cm. long 75. *V. candida*
 - 6. Scape over 20 cm. long 76. *V. macrantha*
 - 5. Perianth-tube 35–80 mm. long.
 - 7. Leaf-blades 4–7 mm. wide at most.
 - 8. Apex of leaf-blade obtuse; sheaths soon divided into coarse fibers.

77. *V. leucanthos*
 - 8. Apex of leaf-blade filiform-attenuate.
 - 9. Perianth-tube 35–50 mm. long.
 - 10. Scapes about equaling the leaves; caudex rarely to 4 cm. long.

78. *V. cachimbensis*
 - 10. Scapes not more than half as long as the leaves; caudex 50–100 cm. long.
 - 11. The perianth-tube 35–40 mm. long . . . 79. *V. macarenensis*
 - 11. The perianth-tube 45–50 mm. long . . . 80. *V. macrosiphonia*
 - 9. Perianth-tube 60–80 mm. long.
 - 12. Flowers exceeding the leaves; leaf-sheaths spotted with dark brown 81. *V. maculata*
 - 12. Flowers about equaling the leaves or shorter.
 - 13. Leaf-blades glabrous beneath; branches including old leaf-sheaths not over 1 cm. in diameter.
 - 14. Trichomes of the ovary subglobose with a minute black gland on the apex 82. *V. machrisiana*
 - 14. Trichomes of the ovary attenuate toward apex with a broad peltate gland 83. *V. uleana*
 - 13. Leaf-blades lepidote-pilose beneath; branches including old leaf-sheaths 2 cm. or more in diameter . . . (94. *V. tubiflora*)
 - 7. Leaf-blades 8–20 mm. wide.
 - 15. Scapes less than 10 cm. long.
 - 16. Trichomes of the ovary attenuate, the glands distinctly stipitate; scapes 4–6 cm. long 84. *V. panamensis*

16. Trichomes of the ovary ovoid, the glands subsessile; scapes 7–9 cm. long.
17. Caudex simple or few-branched, 1–2 meters high.
85. *V. phantasmagoria*
17. Caudex much branched.
18. Perianth-tube densely glandular 86. *V. dumitiana*
18. Perianth-tube very sparsely glandular . . 87. *V. rhynchocarpa*
15. Scapes 10–30 cm. long.
19. Leaf-sheaths essentially glabrous; tepals rounded; perianth-tube 75 mm. long 88. *V. maudeana*
19. Leaf-sheaths densely vestite at least between the nerves.
20. Apex of leaf-blades rounded 89. *V. annulata*
20. Apex of leaf-blades filiform-acuminate.
21. Flowers exceeding the leaves; leaf-blades densely vestite on both sides, 20 cm. long.
22. Leaf-blades 8 mm. wide, flowers solitary . . 90. *V. velutinos*
22. Leaf-blades 17 mm. wide; flowers at least 3 together.
91. *V. dawsonii*
21. Flowers not exceeding the leaves.
23. Leaf-blades lepidote-pilose on both sides; perianth-tube 65 mm. long 92. *V. cana*
23. Leaf-blades glabrous above.
24. Perianth-tube ca. 40 mm. long 93. *V. lithophila*
24. Perianth-tube 45–80 mm. long 94. *V. tubiflora*

Section I. Vellozia

1. *Vellozia macedonis* Woodson, Ann. Mo. Bot. Gard. 37: 398. 1950.
BRAZIL: Minas Gerais: Mun. Ouro Preto: Saramenha.
2. *Vellozia tenella* Mart. ex Schult. f. in R. & S. Syst. 7: 293. 1826.
Vellozia graminea Pohl, Pl. Bras. 1: 118, pl. 93. 1827.
BRAZIL: Minas Gerais: Inficionado. Vila Rica (Ouro Preto).
3. *Vellozia abietina* Mart. Nov. Gen. & Sp. 1: 14, pl. 6. 1823.
Xerophyta abietina Spreng. Syst. Veg. 4: Cur. Post. 137. 1827.
BRAZIL: Minas Gerais: Itambé. Serra da Lapa.
4. *Vellozia tragacantha* Mart. ex Seubert in Mart. Fl. Bras. 3, pt. 1: 75. 1847.
Xerophyta tragacantha Mart. ex Schult. f. in R. & S. Syst. 7: 290. 1826.
BRAZIL: Minas Gerais: Villa do Rio das Contas. Diamantina. Serra de Caraça.
5. *Vellozia pusilla* Pohl, Pl. Bras. 1: 122, pl. 97. 1827.
BRAZIL: Minas Gerais: Itambé. Serra do Cipó. Diamantina.
- Note: Leaves and habit identical with those of *V. taxifolia*, but stamens numerous and ovary smooth.
6. *Vellozia sellovii* Seubert in Mart. Fl. Bras. 3, pt. 1: 75. 1847.
BRAZIL: No locality. (?) Minas Gerais: Serra da Piedade.
7. *Vellozia plicata* Mart. Nov. Gen. & Sp. 1: 16, pl. 9. 1823.
Xerophyta plicata Spreng. Syst. Veg. 4: Cur. Post. 137. 1827.
BRAZIL: Bahia: Serra de Monte Santo.

8. *Vellozia alata* L. B. Smith, sp. nov.

PLATE 1

A *V. glabra* Mikan, cui affinis, laminis foliorum basi grosse brunneociliatis, capsula alato-trigona viride vix lucida differt.

Caudex simple (?), terete and 5 cm. in diameter including the old leaf-sheaths; leaves many-ranked, very densely imbricate, the complete ones about 40 at the apex of the stem; sheaths very closely nerved, suboblong, 7 cm. long, glabrous, the apices recurved with age but remaining entire; blades linear, filiform-acuminate, 4 dm. long, 12 mm. wide at base, densely and strongly nerved on both sides, otherwise even, coarsely brown-ciliate on the slightly thickened margins but not on the inconspicuous keel, otherwise glabrous; scapes few or solitary, erect or decurved, to 16 cm. long, trigonous, glabrous; capsule broadly ellipsoid, 5 cm. long, 3 cm. wide, alate-trigonous, sublustrous, yellow-green when dry; stamens 12 or more; style 5 cm. long.

Type in the U.S. National Herbarium, No. 2340342, collected 3½ miles from Hotel Chapéu do Sol, Serra do Cipó, State of Minas Gerais, Brazil, altitude 1110 meters (3700 feet), December 19, 1959, by Bassett Maguire, C. K. Maguire and J. Murça Pires (No. 44690). Isotype in the New York Botanical Garden.

9. *Vellozia glabra* Mikan, Delect. Fl. & Faun. Brasil. fasc. 2. 1820; Spreng. Syst. Veg. 3: 338. 1826.

Vellozia Vand. Fl. Lusit. & Brasil. Spec. 32, pl. 2. 1788. Without indication of species.

Vellozia phalocarpa Pohl, Pl. Brasil. 1: 123, pl. 98. 1827.

?*Vellozia crassirama* Goeth. & Henr. Blumea 2: 368. 1937.

BRAZIL: Minas Gerais: Serra do Cipó, Diamantina, Sêrro. Itambé. Goiás. Bolivia.

10. *Vellozia incurvata* Mart. ex Schult. f. in R. & S. Syst. 7: 293. 1826.

BRAZIL: Minas Gerais.

11. *Vellozia compacta* Mart. ex Schult. f. in R. & S. Syst. 7: 293. 1826.

Vellozia compacta var. *obtusiflora* and var. *acutiflora* Seubert in Mart. Fl. Bras. 3, pt. 1: 77. 1847.

BRAZIL: Minas Gerais: Piedade, Nova Lima. Serra do Cipó.

12. *Vellozia verruculosa* Mart. ex Schult. f. in R. & S. Syst. 7: 293. 1826.

BRAZIL: Minas Gerais, Goiás: Corumbá. Natividade. Mato Grosso.

13. *Vellozia fibrosa* Goeth. & Henr. Blumea 2: 370. 1937.

BRAZIL: Minas Gerais: Biribiri, near Diamantina.

14. *Vellozia variabilis* Mart. ex Schult. f. in R. & S. Syst. 7: 293. 1826.**14a. *Vellozia variabilis* var. *variabilis***

?*Vellozia alutacea* Pohl, Pl. Bras. 1: 130. 1827.

Capsule tuberculate on the angles only.

BRAZIL: Minas Gerais: Lagoa Grande. Goiás: Serra Dourada.

14b. *Vellozia variabilis* var. *tuberculata* Seubert in Mart. Fl. Bras. 3, pt. 1: 77. 1847.

Capsules with a row of tubercles on each side as well as on angles.

BRAZIL: Minas Gerais: Nova Lima. Caldas.

15. *Vellozia ambigua* Goeth. & Henr. *Blumea* 2: 364. 1937.
BRAZIL: Minas Gerais: Itacolumi.
16. *Vellozia martiana* Goeth. & Henr. *Blumea* 2: 376. 1937.
BRAZIL: Minas Gerais: Pico Itabira do Campo.
17. *Vellozia wettsteinii* Goeth. & Henr. *Blumea* 2: 383. 1937.
BRAZIL: São Paulo: Between Sacramento and Jaguará.
18. *Vellozia angustifolia* Goeth. & Henr. *Blumea* 2: 365. 1937.
BRAZIL: Goiás (?): Morro Cubatão. Minas Gerais: Diamantina.
19. *Vellozia virgata* Goeth. & Henr. *Blumea* 2: 382. 1937.
BRAZIL: Minas Gerais: São José (João?) del Rei. Pico Itabira do Campo.
20. *Vellozia echinata* Goeth. & Henr. *Blumea* 2: 369. 1937.
BRAZIL: Minas Gerais: Caraça.
21. *Vellozia fimbriata* Goeth. & Henr. *Blumea* 2: 371. 1937.
BRAZIL: Minas Gerais: Serra da Lapa.
22. *Vellozia intermedia* Seubert *in* Mart. *Fl. Bras.* 3, pt. 1: 78. 1847.
BRAZIL: Without locality. ?Minas Gerais: Serra do Cipó.
23. *Vellozia barbaceniifolia* Seubert *in* Mart. *Fl. Bras.* 3, pt. 1: 79. 1847.
BRAZIL: Without locality.
24. *Vellozia hemisphaerica* Seubert *in* Mart. *Fl. Bras.* 3, pt. 1: 80. 1847.
BRAZIL: Bahia.
25. *Vellozia breviscapa* Mart. ex Schult. f. *in* R. & S. *Syst.* 7: 293. 1826.
BRAZIL: Minas Gerais: Diamantina.
26. *Vellozia squalida* Mart. ex Schult. f. *in* R. & S. *Syst.* 7: 292. 1826.
BRAZIL: Minas Gerais: Serra do Cipó.
27. *Vellozia aloifolia* Mart. *Nov. Gen. & Sp.* 1: 15, pl. 7. 1823.
BRAZIL: Minas Gerais: Serra de Itambé. Tejuco. Diamantina.
28. *Vellozia viannae* L. B. Smith, sp. nov. PLATE 9, FIGURE 1

A *V. variabile* Mart. ex Schult. f., cui affinis, ovario omnino regulariterque glanduloso differt.

Caudex simple (?), terete and 5 cm. in diameter (including the old leaf-sheaths); leaves many-ranked, very densely imbricate; leaf-sheaths oblong, over 4 cm. long, very densely nerved, dark castaneous with a thin stramineous margin, the apices recurved with age; leaf-blades over 20 before falling, linear, filiform-acuminate, imperfectly known but probably 5 dm. long, 15 mm. or wider, setose-serrate on the scarcely thickened margins, otherwise glabrous, densely nerved, the keel broad but not prominent; scapes slender, 12–15 cm. long, densely dark-glandular toward apex; ovary ellipsoid, 8–10 mm. long, densely and finely dark-glandular throughout; tepals elliptic, rounded and apiculate, 45 mm. long, stamens ca. 18, the phalanges appendaged; anthers subequal, 11 mm. long.

Type in the U.S. National Herbarium, No. 2323056, collected 6 kilometers north of Palácio, Serra do Cipó, Município of Jaboticatubas, State of Minas Gerais, Brazil, October 1953, by F. Segadas-Vianna and J. Lorêdo, Jr. (No. Serra-II, 1103).

29. *Vellozia glandulifera* Goeth. & Henr. *Blumea* 2: 372. 1937.
BRAZIL: Minas Gerais: Cachoeira.
30. *Vellozia scoparia* Goeth. & Henr. *Blumea* 2: 380. 1937.
BRAZIL: Minas Gerais: Parauna and Tejuco. Cachoeira.
31. *Vellozia pilosa* Goeth. & Henr. *Blumea* 2: 377. 1937.
BRAZIL: Minas Gerais: Diamantina.
32. *Vellozia taxifolia* (Mart. ex Schult. f.) Mart. ex Seubert in Mart. *Fl. Bras.* 3, pt. 1: 75. 1847.
Xerophyta taxifolia Mart. ex Schult. f. in R. & S. *Syst.* 7: 291. 1826.
BRAZIL: Minas Gerais: Serra do Cipó. Serra Frio.
33. *Vellozia declinans* Goeth. & Henr. *Blumea* 2: 369. 1937.
BRAZIL: Minas Gerais: Serra da Lapa.
34. *Vellozia barbata* Goeth. & Henr. *Blumea* 2: 366. 1937.
BRAZIL: Minas Gerais: Diamantina.
35. *Vellozia pleurocarpa* Goeth. & Henr. *Blumea* 2: 377. 1937.
BRAZIL: Minas Gerais: Biribiri near Diamantina.
36. *Vellozia leptopetala* Goeth. & Henr. *Blumea* 2: 374. 1937.
BRAZIL: Minas Gerais: Biribiri near Diamantina.
37. *Vellozia resinosa* Mart. ex Schult. f. in R. & S. *Syst.* 7: 293. 1826, emend. L. B. Smith.

Ab omnibus speciebus sectionis *Velloziae* vaginis foliorum apice albo-lanatis, laminis subtus subdense setosis, et ovario dense glanduloso differt.

Caudex simple, very short, terete and 2 cm. in diameter (including the old leaf-sheaths); leaves densely many-ranked; sheaths suboblong, 35 mm. long, dark castaneous with a pale thin margin, lustrous, the exposed apex densely white-lanate, remaining entire; blades about 12 before falling, suberect, linear, subacute, more or less complicate, 15 cm. long, 10 mm. wide, glabrous above, subdensely setose beneath, ciliate; scapes 1-2, slender, 13-15 cm. long, densely dark-glandular toward apex; ovary globose, densely dark-glandular; tepals elliptic, obtuse, 50 mm. long, purple; stamens ca. 12, 15 mm. long.

BRAZIL: Minas Gerais: *Martius* (M, type; F, photo no. 18982). Serra do Cipó, between km. 111 and 128, alt. 1140 m., December 20, 1959, *Maguire & Pires* 44694 (NY, US).

38. *Vellozia brevifolia* Seubert in Mart. *Fl. Bras.* 3, pt. 1: 84, pl. 10, fig. 2. 1847.
BRAZIL: Without locality.
39. *Vellozia epidendroides* Mart. ex Schult. f. in R. & S. *Syst.* 7: 292. 1826.
? *Vellozia variegata* Goeth. & Henr. *Blumea* 2: 381. 1937.
BRAZIL: Minas Gerais: Serra do Cipó. Diamantina. Carangola.
40. *Vellozia minima* Pohl, *Pl. Bras.* 1: 119, pl. 94. 1827.
BRAZIL: Minas Gerais: Itambé. Serra do Cipó. Diamantina. Guinda.
41. *Vellozia streptophylla* L. B. Smith, sp. nov.

PLATE 2; PLATE 9, FIGURES 2, 3

A *V. minima* Pohl, cui affinis, caulibus validioribus, laminis foliorum valde contortis latioribus longe setosis differt.

Caudex erect, much branched, less than 2 dm. high, 7 mm. in diameter; leaves more than 3-ranked, densely imbricate; sheaths very closely nerved, glabrous, erect, entire in age; blades linear, narrowly obtuse, 3 cm. long, 3 mm. wide, subdensely setose, at first erect but recurved and contorted with age, long-persistent; scapes solitary but soon axillary and long-persistent, 25 mm. long, very slender, glandular especially toward apex; capsule globose, 5–6 mm. long, subdensely and evenly glandular; tepals, stamens, and style unknown.

Type in the New York Botanical Garden, collected in the vicinity of Diamantina, State of Minas Gerais, Brazil, 1840, by George Gardner (No. 5233).

42. *Vellozia cryptantha* Seubert in Mart. Fl. Bras. 3, pt. 1: 80. 1847.

BRAZIL Minas Gerais: Diamantina.

43. *Vellozia ramosissima* L. B. Smith, sp. nov.

PLATE 9, FIGURES 4, 5

V. asperula Mart. atque *V. leptopetala* Goeth. & Henr. affinis, a priore foliis retusis, earum vaginis vetustis integris, a posteriore foliorum vaginis vix exsertis, a ambobus caudice maxima ramosissima, foliorum laminis latioribus distinguenda.

Caudex to 2 meters high, slender, the branches 1 cm. in diameter including the old leaf-sheaths; leaves many-ranked, very densely imbricate, the complete ones about 10 at the apex of each branch; sheaths very closely nerved, broadly ovate, amplexicaul, ca. 4 cm. long, glabrous, remaining entire; blades linear, deeply and asymmetrically retuse, 7–9 cm. long, 5 mm. wide, densely nerved, obscurely serrulate on the margins and keel; scapes solitary, about equaling the leaves, decurved at apex with age, slender, trigonous, deeply sulcate, scabrous especially toward apex; capsule stoutly ellipsoid, 12–14 mm. long, subdensely scabrous with fine pale subacute trichomes; tepals linear-spatulate, acute, 23 mm. long; stamens 15–20.

Type in the U.S. National Herbarium, No. 2340340, collected on the Serra do Cipó 2½ miles from Hotel Chapeu de Sol, Minas Gerais, Brazil, altitude 1110 meters, December 19, 1959, by Bassett and Celia K. Maguire and J. Murça Pires (No. 44666). Isotype in the New York Botanical Garden.

44. *Vellozia asperula* Mart. Nov. Gen. & Sp. 1: 15, pl. 8. 1823.

44a. *Vellozia asperula* var. *asperula*

Vellozia papillosa Pohl, Pl. Bras. 1: 128. 1827.

Leaf-blades 12–20 cm. long, about equaling the flowers to somewhat exceeding them, 3–4 mm. wide.

BRAZIL: Minas Gerais: Tres Barras. Tejuco. Itambé.

44b. *Vellozia asperula* var. *filifolia* L. B. Smith, var. nov.

A var. *asperula* foliis valde elongatis flores superantibus, laminis angustissimis differt.

Leaf-blades over 30 cm. long, much exceeding the flowers, only 1 mm. wide.

Type in the New York Botanical Garden, collected on the Serra do Caraça, State of Minas Gerais, Brazil, January 18, 1921, by F. C. Hoehne (No. 5025 in hb. SP).

45. *Vellozia punctulata* Seubert in Mart. Fl. Bras. 3, pt. 1: 82. 1847.

BRAZIL: Bahia.

46. *Vellozia bradei* Schulze-Menz ex Markgraf, Notizblatt 15: 215. 1940.

BRAZIL: Minas Gerais: East of Montes Claros and north of Grão Mogul.

47. *Vellozia piresiana* L. B. Smith, sp. nov. PLATE 9, FIGURES 6, 7

A *V. ornata* Mart. ex Schult. f., cui affinis, foliorum vaginis vix fissis, laminis integris latis differt.

Caudex branching, terete and 3 cm. in diameter (including the old leaf-sheaths); leaves many-ranked, very densely imbricate; leaf-sheaths 4 cm. long, stramineous, lustrous, remaining entire, the nerves nearly contiguous; blades about 15 before falling, erect, linear, attenuate to an obtuse asymmetric apex, 18 cm. long, 12 mm. wide, glabrous, glaucous beneath, the thickened margins entire; scapes slender, to 13 cm. long above the leaf-sheaths, scabrous especially toward apex; ovary ellipsoid, subdensely scabrous; tepals 20 mm. long, violet (! Black & Pires); stamens 15 (?); ovary 13 mm. long.

Type in the Instituto Agrônômico do Norte, No. 69981, collected on the Serra do Cipó at kilometer 132, State of Minas Gerais, Brazil, April 4, 1951, by G. A. Black and J. M. Pires (No. 51-12157).

48. *Vellozia ornata* Mart. ex Schult. f. in R. & S. Syst. 7: 293. 1826.

BRAZIL: Minas Gerais.

49. *Vellozia granulata* Goeth. & Henr. Blumea 2: 373. 1937.

BRAZIL: Minas Gerais: Curalinho near Diamantina. Biribiri near Diamantina.

50. *Vellozia flavicans* Mart. ex Schult. f. in R. & S. Syst. 7: 293. 1826.

Vellozia squamata Pohl, Pl. Bras. 1: 124, pl. 99. 1827.

BRAZIL. Minas Gerais: Itambé. Goiás: Serra Dourada. Anapolis.

51. *Vellozia glauca* Pohl, Pl. Bras. 1: 125, pl. 100. 1827.

- 51a. *Vellozia glauca* var. *glauca*

Vellozia glauca var. *genuina* Seubert in Mart. Fl. Bras. 3, pt. 1: 79. 1847.

Vellozia hamosa Pohl ex Seubert in Mart. Fl. Bras. 3, pt. 1: 79. 1847.

Nomen.

Scape elongate, completely glabrous.

BRAZIL: Goiás: Aldea Carretão de Pedro Terceiro. Chapada dos Veadeiros.

- 51b. *Vellozia glauca* var. *cujabensis* Seubert in Mart. Fl. Bras. 3, pt. 1: 79. 1847.

Scape short, furfuraceous-hirsute toward apex.

BRAZIL: Mato Grosso: Cuyaba.

52. *Vellozia glochidea* Pohl, Pl. Bras. 1: 129. 1827.

BRAZIL: Goiás: Serra Dourada. Rio Araguáia.

53. *Vellozia gardneri* Goeth. & Henr. Blumea 2: 371. 1937.

BRAZIL: Goiás: Natividade.

54. *Vellozia crassicaulis* Mart. ex Schult. f. *in* R. & S. Syst. 7: 292. 1826.

Vellozia albiflora Pohl, Pl. Bras. 1: 121, pl. 96. 1827.

BRAZIL: Minas Gerais: Arraial da Nossa Senhora de Penha. Mendanha.

55. *Vellozia sulphurea* Pohl, Pl. Bras. 1: 120, pl. 95. 1827.

BRAZIL: Minas Gerais: Arraial de São João Baptista. Between Tapanhoacanga and Padre Bento.

56. *Vellozia seubertiana* Goeth. & Henr. Blumea 2: 380. 1937.

BRAZIL: Mato Grosso: Cuyaba; Buriti in the Serra da Chapada.

57. *Vellozia froesii* L. B. Smith, sp. nov.

PLATE 3

A *V. seubertiana* Goeth. & Henr., cui verisimiliter affinis, pedunculo elongato, muricibus ovarii acute truncatis differt.

Caudex and leaf-sheaths unknown but undoubtedly large; leaf-blade linear, filiform-acuminate, to 75 cm. long, 15 mm. wide, antrorsely spinulose-serrate on the pale margins, glabrous; scapes slender, 20–40 cm. long, densely spinulose toward apex; ovary ellipsoid, terete, 20 mm. long, completely covered with slenderly cylindric sharply truncate trichomes; tepals elliptic-spatulate, to 10 cm. long; stamens numerous, shorter than the style; style 7 cm. long.

Type in the Instituto Agronômico do Norte, No. 15,405, collected at Mucugê, Serra da Sincorá, State of Bahia, Brazil, February 1943, by Ricardo de Lemos Fróes (No. 19980). Same, *Fróes* 19979 (NY, paratype).

58. *Vellozia hypoxoides* L. B. Smith, sp. nov.

PLATE 9, FIGURE 8

A *V. pumila* Goeth. & Henr., cui verisimiliter affinis, foliorum marginibus carinaque ciliatis, tepalis subduplo minoribus differt.

Caudex simple or once-branched, 4–10 cm. long, terete and 1 cm. in diameter (including the old leaf-sheaths); leaves densely few-ranked; leaf-sheaths ca. 2 cm. long, dull, with age splitting into coarse fibers; leaf-blades about 10 before falling, recurving, linear, acuminate, 10–11 cm. long, 4 mm. wide, mostly conduplicate, finely ciliate on the margins and keel, otherwise glabrous, densely nerved on both sides; scapes 1–3, very slender, 3–5 cm. long above the leaf-sheaths, densely and finely contorted-setose toward apex; ovary ellipsoid, 5 mm. long, covered with subulate contorted stramineous trichomes; tepals elliptic, obtuse, 2 cm. long, violet; stamens ca. 15, phalanges unappendaged; capsule to 10 mm. long.

Type in the U.S. National Herbarium, No. 2249220, collected on the Serra dos Pirineus, Município of Corumbá, State of Goiás, Brazil, February 17, 1956, by Amaro Macedo (No. 4330). Isotype in the Instituto Agronômico do Norte.

59. *Vellozia pumila* Goeth. & Henr. Blumea 2: 378. 1937.

BRAZIL: Goiás: Ponte Alta.

60. *Vellozia swollenii* L. B. Smith, sp. nov.

PLATE 9, FIGURES 9, 10

A *V. pumila* Goeth. & Henr., cui verisimiliter affinis, foliorum marginibus carinaque integris glabrisque, tepalis subduplo majoribus differt.

Caudex incompletely known, branched, terete and 2 cm. in diameter including the old leaf-sheaths; leaves densely few-ranked; leaf-sheaths ca. 4 cm. long, castaneous, lustrous, soon becoming pectinate-fibrous by the persistence of fine cross-strands on the separating nerves; leaf-blades 7–10 before falling, suberect, linear, acuminate, 30 cm. long, 7 mm. wide, entire, wholly glabrous, the margins thickened, pale; scape solitary, slender, 4 cm. long above the leaf-sheaths, trigonous, densely and finely pale-setose toward apex; ovary ellipsoid, 8 mm. long, covered with pale subulate contorted trichomes; tepals linear-elliptic (?), 80 mm. long; stamens 3 on the unappendaged phalange.

Type in the U.S. National Herbarium, No. 1592031, collected on chapada (dry brushy field), between Barra do Corda and Grajaú, State of Maranhão, Brazil, March 1–5, 1934, by Jason R. Swallen (No. 3617).

61. *Vellozia bulbosa* L. B. Smith, sp. nov.

PLATE 4

A *V. pumila* Goeth. & Henr., cui verisimiliter affinis, planta acaule, foliorum vaginis haud fissis, laminis integris glabrisque, tepalis majoribus differt.

Stemless; leaf-bases forming an irregularly ovoid bulb, 25 mm. long, castaneous, lustrous, densely nerved; blades about 10 before falling, suberect, curved, linear, acuminate, to 24 cm. long, 6 mm. wide, conduplicate, glabrous, the keel and margins pale, thickened, entire; scapes 1–2, slender, 2–3 cm. long above the leaf-sheaths, densely setose-scabrous toward apex; ovary obovoid, 7–9 mm. long, covered with fine subulate contorted stramineous trichomes; tepals linear-elliptic (?), 60 mm. long, pale violet; capsule globose, 18 mm. in diameter, the trichomes becoming thickened and conical.

Type in the Instituto Agronômico do Norte, collected on rocks in savanna, Serra do Cachimbo, State of Pará, Brazil, altitude 425 meters, December 17, 1956, by J. M. Pires, G. A. Black, J. J. Wurdack, and N. T. Silva (No. 6423).

62. *Vellozia cinerascens* Mart. ex Schult. f. *in* R. & S. Syst. 7: 292. 1826.

BRAZIL: Pernambuco: Capoculo. Santa Isabella.

63. *Vellozia circinans* Goeth. & Henr. Blumea 2: 367. 1937.

BRAZIL: Minas Gerais: São João del Rei. Pico da Sander or Pico du Suspiro. Cachoeira do Campo. Serra da Lapa.

64. *Vellozia dasypus* Seubert *in* Mart. Fl. Bras. 3, pt. 1: 81. 1847.

BRAZIL: Bahia: Jacobina. São Salvador. Serra Sincorá.

Further collections may show that this is no more than a variety of *V. cinerascens* which differs only in its glabrous scape. The supposed difference of stamen number is not borne out in the descriptions of the two species in "Flora Brasiliensis."

65. *Vellozia glaziovii* Goeth. & Henr. Blumea 2: 372. 1937.

BRAZIL: Goiás: Serra dos Veadeiros.

66. *Vellozia crinita* Goeth. & Henr. *Blumea* 2: 368. 1937.

BRAZIL: Minas Gerais: São João del Rei.

67. *Vellozia caruncularis* Mart. ex Seubert *in* Mart. *Fl. Bras.* 3, pt. 1: 78, pl. 8, fig. 1. 1847.

BRAZIL: Minas Gerais: Serra do Cipó. Serra do Garimpo. Serra Rola Moça.

68. *Vellozia gracilis* Seubert *in* Mart. *Fl. Bras.* 3, pt. 1: 81, pl. 9. 1847.

BRAZIL: Minas Gerais.

69. *Vellozia grisea* Goeth. & Henr. *Blumea* 2: 373. 1937.

BRAZIL: Between Goiás and Cuyaba.

70. *Vellozia exilis* Goeth. & Henr. *Blumea* 2: 370. 1937.

BRAZIL: Goiás: Chapadão dos Viadeira (?Veadeiros).

Section II. Radia

71. *Vellozia uaipanensis* (Maguire) L. B. Smith, comb. nov.

Barbacenia uaipanensis Maguire, *Mem. N.Y. Bot. Gard.* 9: 477, fig. 117. 1957.

VENEZUELA: Bolívar: Uaipán-tepuí.

72. *Vellozia markgrafii* Schulze-Menz ex Markgraf, *Notizblatt* 15: 216. 1940.

BRAZIL: Minas Gerais: East of Montes Claros.

73. *Vellozia riedeliana* Goeth. & Henr. *Blumea* 2: 379. 1937.

BRAZIL: Minas Gerais: Serra da Lapa.

74. *Vellozia maguirei* L. B. Smith, sp. nov.

PLATE 5

A *V. markgrafii* Schulze-Menz ex Markgraf et *V. riedeliana* Goeth. & Henr., quibus affinis, foliis subtus glabris, pedunculo majore differt.

Caudex to 1 meter high (!Maguire), amount of branching unknown, terete and 3 cm. in diameter at apex (including the old leaf-sheaths); leaf-sheaths 4 cm. long, connate in a funnel for 2 cm., lustrous, densely granular-resinous, densely nerved, the nerves soon separating as coarse fibers; leaf-blades about 12 before falling, suberect, linear, filiform-attenuate, to 28 cm. long, 10 mm. wide at base, densely nerved, resinous, minutely lepidote-ciliate at base on the keel and thickened margins, otherwise glabrous; scape solitary (?), 3 cm. long, glabrous; flowers white; perianth-tube slenderly cylindric and 8 cm. long above the ellipsoid 1 cm. long ovary, 5 mm. in diameter, subdensely glandular; ovary covered with short cylindric gland-tipt trichomes; tepals elliptic, to 5 cm. long.

Type in the U.S. National Herbarium, No. 2340339, collected 49 miles from Diamantina, State of Minas Gerais, Brazil, altitude 1140 meters (3800 feet), December 22, 1959, by Bassett Maguire, C. K. Maguire and J. Murça Pires (No. 44742). Isotype in the New York Botanical Garden.

75. *Vellozia candida* Mikan, *Delect. Fl. & Faun. Brazil.* 2: pl. 1. 1820; text 1825.

Vellozia tertia Spreng. *Neu. Entd.* 2: 108. 1821.

?*Vellozia maritima* Vell. *Fl. Flum.* 219. 1825; *Icon.* 5: pl. 79. 1835. (Rocks, Island of Parati).

BRAZIL: Guanabara: Tijuca. Dois Irmãos. Penha. Corcovado.

76. *Vellozia macrantha* Lem. Ill. Hort. 12: Misc. 41. 1865.

BRAZIL: Without locality.

77. *Vellozia leucanthos* Goeth. & Henr. 2: 375. 1937.

BRAZIL: Minas Gerais: Caraça.

78. *Vellozia cachimbensis* L. B. Smith, sp. nov.

PLATE 6

A *V. macrosiphonia* Taub., cui verisimiliter affinis, caudice brevissimo, pedunculos folias subaequantibus differt.

Plant stemless or sometimes with a caudex up to 4 cm. long and 2 cm. in diameter (including the old leaf-sheaths); leaves densely many-ranked; sheaths ca. 2 cm. long, castaneous, lustrous, white, separating into coarse fibers at apex; blades 20–30 before falling, suberect to spreading, linear, filiform-attenuate, to 14 cm. long, 6 mm. wide, densely nerved, glabrous above, typically lepidote-pilose beneath, setose-ciliate; scape solitary, very slender, about equaling the leaves, densely stipitate glandular toward apex; flowers white (! Pires); perianth-tube slenderly cylindric and 45–65 mm. long above the ellipsoid 5 mm. long ovary, 1–2 mm. in diameter, rather densely glandular; ovary covered with subsessile glands; tepals 4 cm. long; stamens 12 (! Pires).

Type in the Instituto Agronômico do Norte, No. 90.910, collected on rocks, Serra do Cachimbo, State of Pará, Brazil, altitude 425 meters, December 14, 1956, by J. M. Pires, G. A. Black, J. J. Wurdack, and N. T. Silva (No. 6232).

79. *Vellozia macarenensis* Philipson in Schultes, Fam. Velloz. Colomb. in Rev. Acad. Colomb. Cienc. 8, No. 32: 461, pl. 1952.

COLOMBIA: Meta: Sierra de la Macarena.

80. *Vellozia macrosiphonia* Taub. Bot. Jahrb. 21: 424. 1896.

BRAZIL: Goiás: Serra dos Pirineus. Serra Dourada. Serra dos Viadeiros.

81. *Vellozia maculata* Goeth. & Henr. Blumea: 2: 375. 1937.

BRAZIL: Goiás: Cachoeiras da Vargem Grande da Serra da Balisa.

82. *Vellozia machrisiana* L. B. Smith, sp. nov.

PLATE 9, FIGURES 11, 12

A *V. leucantho* Goeth. & Henr., cui affinis, foliis scapoque multo majoribus, foliorum vaginis vetustis haud vel vix fissis differt.

Low, only fruiting material known; caudex simple (?), more or less prostrate (! Dawson), 15 cm. long, terete, 1 cm. in diameter near apex; leaves 3-ranked, very densely imbricate, the complete ones about 12 at the apex of the stem; sheaths sulcate, densely white-sericeous beneath except for the narrow brown lustrous margin, scarcely if at all divided with age, the apices of the upper ones strongly recurved; blades linear, filiform-acuminate, 27 cm. long, 5.5 mm. wide at base, densely and strongly nerved on both sides, otherwise even, ciliate toward base on the thickened margins and rounded keel, otherwise glabrous; scape solitary, extending 18 cm. above the leaf-sheaths, obtusely trigonous, very sparsely vestite toward apex with minute stipitate black glands, capsule ellipsoid, 12 mm. long, strongly

3-lobed, completely covered with minute ovoid gland-tipt trichomes; remains of the perianth-tube slenderly cylindric, 8 cm. long, sparsely and minutely sessile-glandular near base.

Type in the U.S. National Herbarium, No. 2280629, collected on rocks in stream below falls (subject to running water), sandstone area 14 kilometers south of Veadeiros, region of the Chapada dos Veadeiros, ca. lat. 14°30' S., long. 47°30' W., State of Goiás, Brasil, April 25, 1956, by E. Yale Dawson (No. 14674).

83. *Vellozia uleana* L. B. Smith, sp. nov.

PLATE 9, FIGURES 13, 14

A *V. leucantho* Goeth. & Henr., cui affinis, vaginarum nervis subcontiguus, foliis in apicem filiformem attenuatis, ovarii glandulis graciliter stipitatis differt.

Caudex over 23 cm. long, branching at least once, terete and 1 cm. in diameter (including the old leaf-sheaths); leaf-sheaths 4 cm. long, dull, densely nerved, remaining entire and not splitting into fibers, recoiling at apex; leaf-blades about 12 before falling, suberect to spreading, linear, filiform-attenuate, to 25 cm. long, 6 mm. wide, densely nerved, setose-ciliate on the keel and thickened margins when young, glandular-punctate above, glabrous beneath; scape solitary, 9 cm. long above the leaf-sheaths, slender, subdensely stipitate-glandular toward apex; flowers white; perianth-tube slenderly cylindric and 5–7 cm. long above the ellipsoid 8 mm. long ovary, 1.5 mm. in diameter, subdensely glandular; ovary covered with slender gland-tipt trichomes; tepals 4 cm. long.

Type in the Museu Paraense "Emilio Goeldi," No. 13.447, collected on rock faces of the Serra de Uairary (?Mairari), Surumú, Territory of Rio Branco, Brazil, altitude 1000–1200 meters, September 1909, by E. Ule (No. 8372). Isotypes in the New York Botanical Garden and U.S. National Herbarium.

84. *Vellozia panamensis* Standl. Journ. Washington Acad. Sci. 15: 457. 1925.

PANAMA: Chiriquí: Cerro Vaca.

85. *Vellozia phantasmagoria* R. E. Schultes, Bot. Mus. Leaf. Harvard 12: 130, pl. 19, 20. 1946.

COLOMBIA: Vaupés: Mount Chiribiquete.

86. *Vellozia dumitiana* R. E. Schultes, Mutisia No. 12: 2, pl. 1952.

COLOMBIA: Vaupés: Cerro Isibukuri.

87. *Vellozia rhynchocarpa* Goeth. & Henr. Blumea 2: 378. 1937.

BRAZIL: São Paulo: Between Canna Verde and Cajura near Mato Grosso.

88. *Vellozia maudeana* R. E. Schultes, Bot. Mus. Leaf. Harvard 16: 198, pls. 29, 30. 1954.

COLOMBIA: Vaupés: Mesa de Yambí.

89. *Vellozia annulata* Goeth. & Henr. Blumea 2: 365. 1937.

BRAZIL: Goiás: Cachoeira da Vargem Grande. Serra dos Veiadados (?Veadeiros).

90. *Vellozia velutinos*a Goeth. & Henr. Blumea 2: 382. 1937.

BRAZIL: Goiás: Cabeceira (headwaters) do Rio Santa Ana.

91. *Vellozia dawsonii* L. B. Smith, sp. nov.

PLATE 7

A *V. velutinos*a Goeth. & Henr., cui verisimiliter affinis, foliorum laminis subduplo latioribus, floribus haud solitariis differt.

Caudex incompletely known, 25 mm. in diameter (including the old leaf-sheaths); leaves densely many-ranked; sheaths 4 cm. long, densely white-lanate; blades over 30 before falling, linear-triangular, filiform-attenuate, 20 cm. long, 17 mm. wide, finely lepidote-pilose on both sides, flat, densely and minutely ciliate; scapes at least 3 together, slender, about equaling the leaves, densely stipitate-glandular toward apex; flowers white; perianth-tube slenderly cylindric, 70–80 mm. long above the ellipsoid 10 mm. long ovary, 4–5 mm. in diameter, subdensely glandular; ovary covered with slenderly stipitate glands; tepals elliptic, acute, 7 cm. long; anthers 15 mm. long.

Type in the U.S. National Herbarium, No. 2279791, collected on sandstone outcrop 7 kilometers south of Veadeiros, region of the Chapada dos Veadeiros, ca. lat. 14°30' S., long. 47°30' W., State of Goiás, Brasil, April 24, 1956, by E. Yale Dawson (No. 14580).

92. *Vellozia cana* Goeth. & Henr. *Blumea* 2: 367. 1937.

BRAZIL: Goiás: Paranana.

93. *Vellozia lithophila* R. E. Schultes, *Fam. Velloz. Colomb. in Rev. Acad. Colomb. Cienc.* 8, No. 32: 459, pl. 1950.

COLOMBIA: Vaupés: Mesa La Lindosa. San José del Guaviare. Cerro Yapobodá. Cerro Kañendá. Rio Parana Pichuna.

94. *Vellozia tubiflora* (A. Rich.) H. B. K. *Nov. Gen. & Sp.* 7: 155. 1824.

Radia tubiflora A. Rich. *in Kunth, Syn. Pl. Aeq.* 1: 300. 1822.

Barbacenia alexandrinae Rob. Schomb. *Barbacenia Alexandrinae* 13, pl. 1845; Rob. Schomb. *ex Hook. London Journ. Bot.* 4: 13. 1845.

Barbacenia tubiflora Jackson, *Ind. Kew.* 4: 1269. 1895. Wrongly attributed to Benth. & Hook. *Gen.* 3: 740. 1883, who made the combination only inferentially and not validly.

Vellozia alexandrinae Goeth. & Henr. *Blumea* 2: 363. 1937.

VENEZUELA: Amazonas and Bolívar. Brazil: Pará. British Guiana.

The only distinction encountered in the descriptions of *Vellozia tubiflora* and *V. alexandrinae* is the height and branching of the caudex. *Vellozia tubiflora* from along the Rio Orinoco is described as low and slightly branched while *V. alexandrinae* from Mount Roraima is 3 to 4 meters high and much branched. However, Dr. J. J. Wurdack, who has observed *V. tubiflora* in the type area, assures me that it varies according to age and attains great size also.

2. *Barbaceniopsis*

Barbaceniopsis L. B. Smith, gen. nov.

Caulescens, simplex vel ramosus; caudice foliorum vaginis vetustis omnino oblecto; foliis novellis terminalibus, laminis linearibus, haud

regulariter deciduis; scapis terminalibus, unifloris; tepalis 6, subaequalibus, tubum epigynum formantibus; staminibus 6; filamentis brevissimis, teretibus, haud appendiculatis; antheris dorsifixis; ovario infero; styli parte stigmatifera subcylindrica.

Type species: *Barbaceniopsis boliviensis* (Baker) L. B. Smith.

Key to the Species of *Barbaceniopsis*

1. Leaf-blades even, cinereous beneath, 2–2.5 mm. wide; all tepals merely acute **1. B. boliviensis**
1. Leaf-blades carinate, green beneath, 3.5 mm. wide; outer tepals long-aristate **2. B. vargasiana**

1. *Barbaceniopsis boliviensis* (Baker) L. B. Smith, comb. nov.

PLATE 9, FIGURES 15, 16

Vellozia boliviensis Baker, Mem. Torrey Bot. Club 6: 126. 1896.

Barbacenia boliviensis Hauman, Anal. Mus. Nac. Hist. Nat. Buenos Aires 29: 429. 1917.

Barbacenia castilloni Hauman, Anal. Mus. Nac. Hist. Nat. Buenos Aires 29: 426, pl. 4. 1917.

BOLIVIA: Cochabamba: Near Cochabamba, *Bang* 1134 (K, type; US). Tarija: La Merced near Bermejo, alt. 1700 m., *Fiebrig* 2505 (F).

ARGENTINA: Salta: Cafayate, alt. 1400 m., November 24, 1949, *Araque & Barkley* 19–Ar–366 (F). Same, alt. 1700 m., February 10, 1953, *Hayward* 2512 (US). Jujuy: Tumbaya, Volcan to Loma del Tambo, alt. 2500 m., February 22, 1924, *Schreiter* 2561 (US from hb. Venturi 3445). Tilcara, alt. 2300 m., February 20, 1926, *Venturi* 6847 (US). Capital, Quebrada de Chañi, alt. 1600 m., January 30, 1940, *Schreiter* 10959 (UC). Tucumán: Tafi, El Bañado, Quebrada de las Cañas, alt. 2140 m., February 1913, *Castillon* 3245 (BA). Calchaquies, El Bañado, Quebrada de las Cañas, alt. 2200 m., January 10, 1917, *Castillon* 58 (US).

Note: I have not examined the type of *Barbacenia castilloni* Hauman, but other material from the same region shows no essential difference from *Vellozia boliviensis* Baker.

2. *Barbaceniopsis vargasiana* (L. B. Smith) L. B. Smith, comb. nov.

Barbacenia vargasiana L. B. Smith, Bol. Soc. Peru Bot. 1: 13, figs. 1, 2. 1948.

PERU: Cuzco: Anta, between Sisal and Cunyac, *Vargas* 4883 (GH, type; US).

3. *Barbacenia*

Barbacenia Vand. Fl. Lusit. & Brasil. Spec. 21, pl. 1. 1788.

Pleurostima Raf. Fl. Tellur. 2: 97. 1836.

Visnea Steud. ex Endl. Gen. 173. 1837. Nomen in synonymy.

Plants of small or medium stature; caudex usually simple or few-branched; leaf-blades breaking off irregularly; tepals forming an epigynous tube; stamens 6; filaments evident, flat with 2 lobes or appendages at the summit; anthers dorsifixes; stigmas inconspicuous, not peltate nor broadly lobed.

Type species: *Barbacenia brasiliensis* Willd.

Keys to the Species of Barbacenia

1. Perianth-tube not more than twice as long as the ovary.
 2. Ovary section of the perianth partly or wholly glabrous, the costae evident (lacking in *B. beauverdii*) SUBKEY I
 2. Ovary section of the perianth wholly vestite SUBKEY II
1. Perianth-tube more than twice as long as the ovary SUBKEY III

SUBKEY I

1. Perianth-tube completely glabrous.
 2. Tube of the perianth smooth, ecostate 1. *B. beauverdii*
 2. Tube of the perianth costate.
 3. Costae of the perianth 18; caudex very short; leaf-blades 11 cm. long, 10 mm. wide 2. *B. brachycalyx*
 3. Costae of the perianth 12; caudex to 30 cm. long; leaf-blades 7-8 cm. long, 2.5 mm. wide 3. *B. caricina*
1. Perianth-tube vestite on the costae.
 4. Indument of the perianth of pointed trichomes, eglandular.
 5. Anthers twice as long as the filaments 4. *B. squamata*
 5. Anthers exceeded by the filament-appendages.
 6. Tepals 40 mm. long, ample; leaf-blades 9 mm. wide . . . 5. *B. rogieri*
 6. Tepals 20-30 mm. long, narrow.
 7. Leaf-blades 5 mm. wide 6. *B. gaveensis*
 7. Leaf-blades 7-9 mm. wide 7. *B. seubertiana*
 4. Indument of the perianth of sessile (verruculose) or of stipitate glands.
 8. Anthers equaling or exceeding the filament-appendages.
 9. Leaf-blades 2 mm. wide; perianth-tube 8 mm. long.
 8. *B. stenophylla*
 9. Leaf-blades 6-18 mm. wide; perianth-tube 13-20 mm. long.
 10. Perianth-tube about twice as long as the ovary; leaf-blades 12-18 mm. wide 9. *B. inclinata*
 10. Perianth-tube not more than half again as long as the ovary.
 11. Scape 35 cm. long; leaf-blades 10-18 mm. wide.
 10. *B. longiscapa*
 11. Scape ca. 15 cm. long; leaf-blades 4-11 mm. wide.
 12. Leaf-blades 9-11 mm. wide; filaments 8 mm. long.
 11. *B. flavida*
 12. Leaf-blades 4-8 mm. wide.
 13. Tepals glandular-punctate; costae wholly covered by black stipitate glands 12. *B. irwiniana*
 13. Tepals glabrous; costae laxly glandular or the intermediate ones glabrous.
 14. Filaments 7-8 mm. long, only slightly shorter than the anthers; leaves distributed along the stem.
 13. *B. foliosa*
 14. Filaments ca. 4 mm. long, about half as long as the anthers; leaves clustered at apex of stem (perianth-tube described as glandular, but not so depicted) . . (4. *B. squamata*)
 8. Anthers exceeded by the filament-appendages.
 15. Scape 1 cm. long; perianth-tube about twice as long as the ovary and forming a slender tube above it; anthers medifixed. . 14. *B. goethartii*

15. Scape elongate; perianth-tube much less than twice as long as the ovary and forming a broad cylinder above it.

16. Leaf-blades 6–8 cm. long, only $\frac{1}{3}$ – $\frac{1}{2}$ as long as the scapes, 2–4 mm. wide; anthers equaling the base of the filament-sinus.

15. **B. brevifolia**

16. Leaf-blades more than twice as large, more than half as long as the scape and mostly exceeding it.

17. The leaf-blades entire; costae bearing stipitate glands; style subulate, scarcely dilated by the sigmas . 16. **B. mantiqueirae**

17. The leaf-blades denticulate or spinulose-serrate.

18. Tepals 40 mm. long, ample; leaf blades 9 mm. wide (perianth-tube described as glandular, but not so depicted).

(5. **B. rogieri**)

18. Tepals 16–20 mm. long, narrow.

19. Leaf-blades with narrow dark margins and keel, denticulate; stigmas apical, making the style slenderly conical.

17. **B. nigrimarginata**

19. Leaf-blades concolorous.

20. Stigmas apical on the style, making it clavate; anthers acuminate, exceeding the base of the sinus; leaf-blades denticulate 18. **B. gounelleana**

20. Stigmas submedian on the style; anthers rounded-apiculate; leaves spinulose-serrate. 19. **B. purpurea**

SUBKEY II

1. Indument of the perianth wholly of pointed trichomes, not glandular.

2. Tepals only about $\frac{1}{2}$ as long as the tube; leaf-blades hirsute beneath.

20. **B. schwackei**

2. Tepals 1–2 times as long as the tube; leaf-blades glabrous . . 21. **B. fulva**

1. Indument of the perianth glandular, either sessile or stipitate.

3. Scapes up to 12 per rosette; leaves up to 40; sheaths resinous-conglutinated; flowers violet; tepals 4–5 mm. long 22. **B. polyantha**

3. Scapes 1–5 per rosette.

4. Leaf-blades uniformly vestite.

5. Ovary trigonous, verrucose 23. **B. trigona**

5. Ovary terete or if subtrigonous then covered with stipitate glands.

6. Flowers yellow; perianth-tube 12 mm. long, twice as long as the ovary 24. **B. globata**

6. Flowers red to lilac, or white.

7. Glands of the perianth-tube sessile; perianth-tube twice as long as the ovary 25. **B. coccinea**

7. Glands of the perianth-tube stipitate.

8. Leaf-indument glandular.

9. Tepals 7 mm. long; flowers red 26. **B. glutinosa**

9. Tepals 17–20 mm. long; flowers white . . 27. **B. markgrafii**

8. Leaf-indument eglandular.

10. Perianth-tube 25 mm. long; flowers red . . . 28. **B. ignea**

10. Perianth-tube 20 mm. long; flowers lilac . . 29. **B. lilacina**

4. Leaf-blades glabrous except for the margins and keel.

11. Glands of the ovary sessile; perianth-tube 50 mm. long; anthers medifixed, nearly twice as long as the filaments; flowers yellow . 30. **B. vandellii**

11. Glands of the ovary stipitate.
12. Anthers equaling the filament-appendages; flowers yellow. 31. *B. brasiliensis*
12. Anthers exceeding the filament-appendages.
13. Trichomes of the upper scape long, slender, mostly or entirely eglandular; tepals 9–11 mm. long.
14. Flowers deep lilac; leaf-blades 10 mm. wide . 32. *B. hirtiflora*
14. Flowers yellow; leaf-blades 7 mm. wide . . 33. *B. williamsii*
13. Trichomes of the upper scape short, stout, coarsely glandular; tepals 15–17 mm. long.
15. Epigynous tube subcylindric; perianth-tube 20–23 mm. long. 34. *B. flava*
15. Epigynous tube campanulate; perianth-tube 25–32 mm. long.
16. Perianth-tube 32 mm. long; caudex 3–4 dm. high. 35. *B. glauca*
16. Perianth-tube 25 mm. long; caudex very short.
17. Leaf-blades 40 cm. long, 8–10 mm. wide, glaucous. 36. *B. itabirensis*
17. Leaf-blades 9–16 cm. long, 4–7 mm. wide, green (?). 37. *B. sellovii*

SUBKEY III

1. Epigynous tube infundibuliform, distinctly wider at the mouth than at the base.
2. Tepals broadly ovate, as broad as long; perianth-tube 35 mm. long; flowers subsessile 38. *B. macrantha*
2. Tepals oblong, lanceolate, or elliptic, much longer than broad.
3. Perianth-tube 70–75 mm. long.
4. Tepals reflexed, 40 mm. long; perianth-indument eglandular. 39. *B. rubro-virens*
4. Tepals erect, 20 mm. long; perianth-indument glandular. 40. *B. riedeliana*
3. Perianth-tube 30–55 mm. long.
5. Indument of perianth eglandular; perianth-tube 30 mm. long. 41. *B. luzulifolia*
5. Indument of perianth glandular; perianth-tube 50–55 mm. long.
6. Leaf-blades 9 cm. long, 9 mm. wide; ovary 10 mm. long, $\frac{1}{6}$ – $\frac{1}{5}$ of the perianth-tube 42. *B. viscosissima*
6. Leaf-blades 22 cm. long, 17 mm. wide; ovary 17 mm. long, $\frac{1}{3}$ of the perianth-tube 43. *B. paranaensis*
1. Epigynous tube slenderly cylindric or very slightly enlarged toward apex.
7. Indument of the perianth subulate or lacking.
8. Flowers sessile.
9. Tepals broadly elliptic, 10 mm. long; flowers yellow . . 44. *B. exscapa*
9. Tepals linear, 24 mm. long; flowers red . . . 45. *B. gentianoides*
8. Flowers distinctly scapose.
10. Perianth-tube 50–60 mm. long.
11. Ovary $\frac{1}{3}$ of perianth-tube; scape pilose 46. *B. hilairei*
11. Ovary $\frac{2}{3}$ of perianth-tube.
12. Scares glabrous; perianth-tube 50 mm. long, sparsely pilose on the costae 47. *B. oxytepala*
12. Scares densely tomentellous toward apex; perianth-tube 60 mm. long, densely and evenly gray-tomentellous . . . 48. *B. grisea*

10. Perianth-tube 30–40 mm. long.
13. Plant completely glabrous; tepals ovate or lance-ovate, acute.
49. *B. glabra*
13. Plant vestite.
14. Filaments less than half as long as the anther; tepals erect, 12 mm. long 50. *B. tomentosa*
14. Filaments as long as or longer than the anther, tepals subspreading to reflexed, 15–26 mm. long.
15. Epigynous tube 10 mm. in diameter; tepals reflexed, obtuse.
51. *B. schidigera*
15. Epigynous tube, 3–6 mm. in diameter; tepals subspreading, acute.
16. Perianth-tube densely pubescent; epigynous tube 4–6 mm. in diameter 41. *B. luzulifolia*
16. Perianth-tube very sparsely pubescent and appearing glabrous; epigynous tube 3 mm. in diameter.
52. *B. graciliflora*
7. Indument of the perianth glandular.
17. Glands of the perianth sessile or subsessile.
18. Leaves glabrous except the margins; perianth-glands sessile; tepals 12 mm. long 53. *B. ensifolia*
18. Leaves evenly pilose; perianth glands subsessile; tepals 23 mm. long.
54. *B. glaziovii*
17. Glands of the perianth long-stipitate.
19. Scape exceeding the leaves, its glandular indument of 2 types.
20. Perianth-tube 3 times as long as the ovary . . . 55. *B. conicostigma*
20. Perianth-tube 4–5 times as long as the ovary . . . 56. *B. cuspidata*
19. Scape equaling or shorter than the leaves.
21. Leaf-blades glabrous except the keel and margins.
22. Perianth-tube 65 mm. long; flower yellow . . . 57. *B. longiflora*
22. Perianth-tube 30–50 mm. long.
23. The perianth-tube 5 times as long as the ovary, straight, ecostate 58. *B. gardneri*
23. The perianth-tube 3 times as long as the ovary, curved, costate.
59. *B. curviflora*
21. Leaf-blades evenly vestite.
24. Filaments linear.
25. Tepals 30–35 mm. long 60. *B. fragrans*
25. Tepals 18–20 mm. long.
26. Leaf-blades 4 mm. wide 61. *B. tricolor*
26. Leaf-blades 10 mm. wide 62. *B. blanchetii*
24. Filaments broad.
27. Sinus of the filament shallow; filaments quadrate, 4 mm. long.
63. *B. mollis*
27. Sinus of the filament deep; filaments oblong or broad-based.
28. Indument of the scape white, contrasting sharply with the dark indument of the perianth-tube; perianth-tube 25 mm. long 64. *B. leucopoda*
28. Indument of the scape and perianth-tube uniformly dark; perianth-tube 30–50 mm. long.
29. Filaments oblong, their sides parallel; anthers 8–9 mm. long; leaf-blades uniformly setose-glandular.

30. Leaf-blades 9 mm. wide; anthers exceeding the filaments by less than $\frac{1}{8}$ 65. **B. blackii**
 30. Leaf-blades 5 mm. wide; anthers exceeding the filaments by $\frac{3}{8}$ 66. **B. rubra**
 29. Filaments broad-based, much contracted upward; anthers 12–15 mm. long, exceeding the filaments by $\frac{3}{4}$ or more.
 31. Ovary rounded at base, broadly obovoid. 67. **B. damaziana**
 31. Ovary long-attenuate at base, slenderly obconic. 68. **B. bahiana**
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1. **Barbacenia beauverdii** Damazio, Bull. Herb. Boiss. II. 7: 595, fig. 1907.
 BRAZIL: Minas Gerais: Serra do Frasão.
 2. **Barbacenia brachycalyx** Goeth. & Henr. Blumea 2: 340, fig. A. 1937.
 BRAZIL: Goiás: Pichoa to Morro do Espigão.
 3. **Barbacenia caricina** Goeth. & Henr. Blumea 2: 340, fig. B. 1937.
 BRAZIL: Rio de Janeiro: Nova Friburgo to Pedra do Conego.
 4. **Barbacenia squamata** Hook. Bot. Mag. 71: pl. 4136. 1845.
Vellozia squamata Jackson, Ind. Kew. 4: 1269. 1895, wrongly attributed to Benth. & Hook. Gen. 3: 740. 1883, who made the combination only inferentially and not validly.
 BRAZIL: Rio de Janeiro: Serra dos Orgãos. Guanabara: Morro do Flamengo.
 5. **Barbacenia rogieri** hort. ex Moore & Ayres, Mag. Bot. 2: 209, pl. 1850; Lem. Jard. Fl. 1: pl. 82. 1851.
 SOUTH AMERICA: No locality.
 6. **Barbacenia gaveensis** Goeth. & Henr. Blumea 2: 346. 1937.
 BRAZIL: Guanabara: Gavea. Tijuca.
 7. **Barbacenia seubertiana** Goeth. & Henr. Blumea 2: 360. 1937.
Barbacenia purpurea Hook. var. *minor* Seubert in Mart. Fl. Bras. 3, pt. 1: 68. 1847.
 BRAZIL: Rio de Janeiro: Serra dos Orgãos, Faboinha. Guanabara: Gavea.
 8. **Barbacenia stenophylla** Goeth. & Henr. Blumea 2: 361, fig. F. 1937.
 BRAZIL: Goiás: Morro do Salto.
 9. **Barbacenia inclinata** Goeth. & Henr. Blumea 2: 352. 1937.
 BRAZIL: Minas Gerais: Diamantina.
 10. **Barbacenia longiscapa** Goeth. & Henr. Blumea 2: 355. 1937.
 BRAZIL: Minas Gerais: Serra da Lapa.
 11. **Barbacenia flavida** Goeth. & Henr. Blumea 2: 343. 1937.
 BRAZIL: Minas Gerais. Goiás: Pichoa to Morro do Espigão.
 12. **Barbacenia irwiniana** L. B. Smith, sp. nov. PLATE 10, FIGURES 17, 18

A *B. foliosa* Goeth. & Henr., cui affinis, tepalis glanduloso-punctatis, ovarii costis glandulis nigris stipitatis omnino obtectis differt.

Caudex 3 cm. long with roots almost throughout; leaves numerous, 3-ranked; sheaths ovate, 1 cm. long, very closely nerved, glabrous; blades linear, acuminate, 13–15 cm. long, 4 mm. wide, closely nerved

on both sides, sparsely denticulate on keel and margins, otherwise smooth and glabrous; scape solitary, about equaling the leaves, slender, bearing black stipitate glands especially near apex; perianth-tube 15 mm. long; ovary ellipsoid, the costae covered with black stipitate glands; epigynous tube infundibuliform, 4 mm. high; tepals suberect at anthesis, lanceolate, subacute, 13 mm. long, yellow (!Irwin), reddish when dry, the outer slightly narrower; filaments 6 mm. long, the oblong rounded appendages about twice as long as the quadrate base; anthers linear, 8 mm. long, slightly exceeding the filament-appendages.

Type in the U.S. National Herbarium, No. 2324659, collected in narrow crevice among rocks on steep slope, Pico da Bandeira, Serra Caparao, State of Minas Gerais, Brazil, at 2700 meters (9000 feet) altitude, March 3, 1959, by H. S. Irwin (No. 2803).

13. *Barbacenia foliosa* Goeth. & Henr. Blumea 2: 344, fig. D. 1937.

BRAZIL: Guanabara: Tijuca.

14. *Barbacenia goethartii* Henr. Blumea 2: 350, fig. K. 1937.

BRAZIL: Minas Gerais: Penha (?).

15. *Barbacenia brevifolia* Taub. Bot. Jahrb. 12, Beibl. 27: 2. 1890.

BRAZIL: No locality.

16. *Barbacenia mantiqueirae* Goeth. & Henr. Blumea 2: 355. 1937.

BRAZIL: São Paulo: Serra da Mantiqueira.

17. *Barbacenia nigrimarginata* L. B. Smith, sp. nov. PLATE 10, FIGURES 19-22

A *B. gounelleana* Beauverd, cui affinis, foliorum vaginis mox in fibras solutis, laminis nigrimarginatis, filamentorum lobis obtusis, antheris filamentorum sinum apicalem haud attingentibus differt.

Caudex only about 2 cm. long; leaves very densely imbricate, glaucous beneath; sheaths 3 cm. long, soon dividing into coarse stiff fibers; blades very narrowly triangular, filiform-acuminate, not at all contracted at base, 25 cm. long, 9 mm. wide, finely and closely nerved on both sides, the thickened margins and keel black and minutely serrulate; scape solitary, 25 cm. long, slender, sulcate, the upper part obscurely glandular; perianth-tube obconic, 17 mm. long, very slightly exceeding the ovary, 5 mm. in diameter, diffusely verruculose; tepals suberect at anthesis, elliptic, obtuse, 22 mm. long, the outer distinctly narrower; filaments narrowly obovate with short rounded lobes, about half as long as the tepals; anthers linear, 6 mm. long, not reaching the base of the sinus.

Type in the U.S. National Herbarium, No. 2279780, collected on stony summit of butte shoulder 5 kilometers west of Veadeiros, region of the Chapada dos Veadeiros, ca. lat. 14°30' S., long. 47°30' W., State of Goiás, Brazil, April 29, 1956, by E. Yale Dawson (No. 14717).

18. *Barbacenia gounelleana* Beauverd, Bull. Herb. Boiss. II. 7: 704. 1907.

BRAZIL: Rio de Janeiro: Itatiaia.

19. *Barbacenia purpurea* Hook. Bot. Mag. 54: pl. 2777. 1827.
Pleurostima purpurea (Hook.) Raf. Fl. Tellur. 2: 97. 1836.
 BRAZIL: Guanabara (?): "Neighborhood of Rio de Janeiro."
20. *Barbacenia schwackei* Goeth. & Henr. Blumea 2: 359, fig. J. 1937.
 BRAZIL: Minas Gerais: Serra do Cipó.
21. *Barbacenia fulva* Goeth. & Henr. Blumea 2: 345, fig. E. 1937.
 BRAZIL: Minas Gerais: No locality.
22. *Barbacenia polyantha* Goeth. & Henr. Blumea 2: 357. 1937.
 BRAZIL: Minas Gerais: Biribiri.
23. *Barbacenia trigona* Goeth. & Henr. Blumea 2: 362. 1937.
 BRAZIL: Minas Gerais: Milho Verde.
24. *Barbacenia globata* Goeth. & Henr. Blumea 2: 349. 1937.
 BRAZIL: Minas Gerais: Rio das Pedras.
25. *Barbacenia coccinea* Mart. ex Schult. f. in R. & S. Syst. 7: 286. 1826.
 BRAZIL: Minas Gerais: Itambé.
26. *Barbacenia glutinosa* Goeth. & Henr. Blumea 2: 350. 1937.
 BRAZIL: Minas Gerais: Morro da Lapa.
27. *Barbacenia markgrafii* Schulze-Menz ex Markgraf, Notizblatt 15: 216. 1940.
 BRAZIL: Minas Gerais: Grão Mogul to Montes Claros.
28. *Barbacenia ignea* Mart. ex Schult. f. in R. & S. Syst. 7: 285. 1826.
 BRAZIL: Minas Gerais: Serra Frio. Sérro.
29. *Barbacenia lilacina* Goeth. & Henr. Blumea 2: 354. 1937.
- 29a. *Barbacenia lilacina* var. *lilacina*
 Leaf-blades hirsute; filaments bifid $\frac{1}{3}$ – $\frac{1}{2}$; flowers lilac.
 BRAZIL: Minas Gerais: Serra do Funil, Rio Paranaha.
- 29b. *Barbacenia lilacina* var. *pallidiflora* Henr. Blumea 2: 354. 1937.
 Leaf-blades sparsely hirsute; filaments bifid more than $\frac{1}{2}$; flowers pale lilac.
 BRAZIL: Minas Gerais: Curralinho to Diamantina.
30. *Barbacenia vandellii* Pohl ex Seubert in Mart. Fl. Bras. 3, pt. 1: 72, pl. 8, fig. 3. 1847.
 BRAZIL: Minas Gerais: São João. Itambé.
31. *Barbacenia brasiliensis* Willd. Sp. Pl. 2: 227. 1799.
Barbacenia Vand. Fl. Lusit. & Brasil. Spec. 21, pl. 1. 1788; Roemer, Script. Hisp. 98, pl. 6, fig. 9. 1796. Without indication of species.
Barbacenia vandelli Schult. f. in R. & S. Syst. 7: 288. 1826. Wrongly attributed to Roemer who cited the genus and its author without any specific name.
Barbacenia bicolor Mart. Nov. Gen. & Sp. 1: 19, pl. 13. 1823.
Visnea Steud. ex Endl. Gen. 173. 1837. Nomen in synonymy, without indication of species.
 BRAZIL: Minas Gerais: Diamantina.
32. *Barbacenia hirtiflora* Goeth. & Henr. Blumea 2: 351, fig. L. 1937.
 BRAZIL: Minas Gerais: Curralinho to Diamantina.
33. *Barbacenia williamsii* L. B. Smith, sp. nov. PLATE 10, FIGURES 23, 24
 A *B. hirtiflora* Goeth. & Henr., cui affinis, floribus aureis, foliorum laminis angustioribus differt.

Caudex very short; leaves numerous, persistent; sheaths ovate, 1 cm. long, glabrous, sulcate; blades linear, filiform-acuminate, to 22 cm. long, 7 mm. wide, closely and finely nerved, dull green, glabrous except for the long-ciliate keel and thickened yellow margins; scapes 1–3, slightly shorter to slightly longer than the leaves, ca. 1 mm. in diameter, sulcate, densely crisp-pilose with slender red-brown mostly eglandular trichomes; perianth-tube 25 mm. long, about twice the ellipsoid ovary and cylindrical above it, 5 mm. in diameter, densely pilose-glandular; tepals suberect at anthesis, oblong, obtuse, 11 mm. long; filaments oblong with long acuminate lobes, nearly equaling the linear anthers.

Type in the Gray Herbarium of Harvard University, collected on iron ore, Serra da Mutuca, near Belo Horizonte, Município of Nova Lima, State of Minas Gerais, Brazil, altitude 1200–1400 meters, April 7, 1945, by Louis O. Williams and Vicente Assis (No. 6696). Isotype in the U.S. National Herbarium, No. 1932777.

BRAZIL: Minas Gerais: Mun. Nova Lima: In rocky slopes, Serra da Mutuca, February 1945, *L. O. Williams* 5201 (GH); 5204 (GH). In campo, Serra do Curral, alt. 1300 m., March 30, 1945, *L. O. Williams & V. Assis* 6386 (GH, US).

34. *Barbacenia flava* Mart. ex Schult. f. *in* R. & S. Syst. 7: 286. 1826.

34a. *Barbacenia flava* var. *flava*

Caudex to 8 cm. long; leaf-blades 13–20 cm. long, 8–12 mm. wide; scapes equaling the leaves; perianth-tube 16 mm. long; tepals 10–12 mm. long.

BRAZIL: Minas Gerais: Itambé. Serra do Cipó.

34b. *Barbacenia flava* var. *minor* L. B. Smith, var. nov.

A var. *flava* omnibus partibus valde minoribus differt.

Caudex 1–4 cm. long; leaf-blades 8–13 cm. long, to 8 mm. wide; scapes shorter than the leaves; perianth-tube 15–20 mm. long; tepals 5 mm. long.

Type in the U.S. National Herbarium, No. 2340345, collected 3½ miles from Hotel Chapeu de Sol, Serra do Cipó, Município Jaboticatubas, State of Minas Gerais, Brazil, altitude 1110 meters (3700 feet), December 19, 1959, by Bassett Maguire, C. K. Maguire and J. Murça Pires (No. 44665). Isotype in the New York Botanical Garden. Paratype, No. 44691, same data (NY, US).

35. *Barbacenia glauca* Mart. ex Schult. f. *in* R. & S. Syst. 7: 288. 1826.

BRAZIL: Minas Gerais: Itambé.

36. *Barbacenia itabirensis* Goeth. & Henr. Blumea 2: 353. 1937.

BRAZIL: Minas Gerais: Pico d'Itabira do Campo.

37. *Barbacenia sellovii* Goeth. & Henr. Blumea 2: 359. 1937.

BRAZIL: Minas Gerais: Serra da Mooda (Moeda?). Serra da Piedade.

38. *Barbacenia macrantha* Lem. Jard. Fl. 4: pl. 390. 1854.

BRAZIL: Minas Gerais: Serra do Cipó.

39. *Barbacenia rubro-virens* Mart. Nov. Gen. & Sp. 1: 20, pl. 4, fig. 1. 1823.

BRAZIL: Minas Gerais: Diamantina.

40. *Barbacenia riedeliana* Goeth. & Henr. *Blumea* 2: 35819. 37.

BRAZIL: Minas Gerais: Serra da Lapa.

41. *Barbacenia luzulifolia* Mart. ex Schult. f. *in* R. & S. *Syst.* 7: 285. 1826.

BRAZIL: Minas Gerais: Ouro Preto.

42. *Barbacenia viscosissima* Goeth. & Henr. *Blumea* 2: 363. 1937.

BRAZIL: Minas Gerais: São João. Itacolumi. Ouro Preto (?).

43. *Barbacenia paranaensis* L. B. Smith, sp. nov. PLATE 10, FIGURES 25, 26

A *B. viscosissima* Goeth. & Henr., cui affinis, foliis ovarioque multo majoribus, tepalis ellipticis latioribus, tubo perianthii ovarium triplo solum longioribus differt.

Caudex over 2 dm. long, terete, 10–15 mm. in diameter at apex (including leaf-sheaths); leaves densely imbricate; sheaths ovate, amplexicaul at base, 3 cm. long, sulcate at apex and margins; blades linear-lanceolate, filiform-acuminate, slightly attenuate toward base, 23–30 cm. long, 17–20 mm. wide, entire, finely nerved, green with the mid-nerve white above, finely and subdensely glandular-pilose on both sides; scape solitary, extending 10–12 cm. above the leaf-sheaths, slender, densely glandular-pilose; perianth-tube 45–55 mm. long, about 3 times as long as the ellipsoid ovary, slightly contracted above the ovary and narrowly campanulate, 15 mm. in diameter at apex, minutely stipitate-glandular, green (! Hatschbach); tepals reflexed at anthesis, broadly elliptic, subacute and apiculate, 17 mm. long; filaments broadly subtriangular with short acute appendages; anthers linear, subbasifixed, 11 mm. long; style exceeding the stamens, broadly ovoid at apex with 3 ovate stigmas.

Type in the U.S. National Herbarium, No. 2279892, collected on sandstone (arenite) bluffs, Fazenda Morungava, Rio de Funil, Município Sengés, State of Paraná, Brazil, December 15, 1958, by G. Hatschbach and R. B. Lange (No. 5359). Isotype in Herbário Hatschbach.

BRAZIL: Paraná: Sengés: Itararé, Morungava, on shady banks in "campo cerrado," alt. 740 m., January 23, 1915, *Dusén* 16478 (F, GH); December 7, 1915, *Dusén* 17379 (F, GH, fruit).

44. *Barbacenia exscapa* Mart. *Nov. Gen. & Sp.* 1: 21, pl. 14. 1823.

BRAZIL: Minas Gerais: Itambé.

45. *Barbacenia gentianoides* Goeth. & Henr. *Blumea* 2: 347, fig. M. 1937.

BRAZIL: Minas Gerais: Rio das Pedras by Valu. Serra da Lapa. As Dattas to Parauna. Serra do Cipó (?).

46. *Barbacenia hilairei* Goeth. & Henr. *Blumea* 2: 351. 1937.

BRAZIL: Minas Gerais: No locality.

47. *Barbacenia oxytepala* Goeth. & Henr. *Blumea* 2: 357. 1937.

BRAZIL: Minas Gerais: Biribiri to Diamantina.

48. *Barbacenia grisea* L. B. Smith, sp. nov.

PLATE 8

A *B. oxytepala* Goeth. & Henr., cui affinis, foliis longe ciliatis, scapo et perigonii tubo densissime adpresseque griseo-tomentellis differt.

Caudex simple, erect, nearly 2 dm. high, covered with the charred remains of old leaves and appearing 5 cm. in diameter; leaves many-ranked, very densely imbricate; sheaths closely sulcate with the nerves almost contiguous, covered with a thick resinous coat; blades linear, attenuate to a filiform apex, 22 cm. long, 13 mm. wide, sulcate on both sides, resinous-punctulate between the nerves, entire, glabrous except the finely long-ciliate margins; scapes 2, 22–26 cm. long, with the perianth very finely and closely gray-tomentellous especially toward apex, scarcely glandular; perianth-tube subcylindric, 60 mm. long; tepals and stamens imperfectly known; ovary 25 mm. long, 5 mm. in diameter, attenuate at base, greatly enlarged in fruit.

Type in the New York Botanical Garden, collected 49 miles from Diamantina, State of Minas Gerais, Brasil, altitude 1140 meters (3800 feet), December 22, 1959, by Bassett Maguire, C. K. Maguire and J. Murça Pires (No. 44745).

49. *Barbacenia glabra* Goeth. & Henr. Blumea 2: 348, fig. H. 1937.

BRAZIL: Minas Gerais: No locality.

50. *Barbacenia tomentosa* Mart. Nov. Gen. & Sp. 1: 18, pl. 11. 1823.

BRAZIL: Minas Gerais: Ouro Preto.

51. *Barbacenia schidigera* Lem. Jard. Fl. 2: pl. 198. 1852.

BRAZIL: Minas Gerais: Pico d'Itacolumi.

52. *Barbacenia graciliflora* L. B. Smith, sp. nov. PLATE 10, FIGURES 27, 28

A *B. schidigera* Lem., cui affinis, tubo epigyno gracili, tepalis subpatentibus acutis differt, et a *B. luzulifolia* Mart., tubo epigyno graciliori subglabro differt.

Caudex simple or few-branched, 8–15 cm. long, 1 cm. in diameter (including the leaf-sheaths); leaves very densely imbricate; sheaths widely sulcate; blades linear, cuspidate-acuminate, slightly narrowed toward base, 11–13 cm. long, 9 mm. wide, dull green, glabrous except for the ciliate margins, rather broadly sulcate with the grooves wider than the nerves; scapes 1–3, extending 4 cm. above the leaf-sheaths, ca. 0.7 mm. in diameter, glabrous; perianth-tube 4 cm. long, more than twice as long as the ellipsoid ovary and contracted above it to a slender tube 3 mm. in diameter, obscurely costate, very sparsely pubescent and appearing glabrous, red (! Williams); tepals subspreading at anthesis, linear, acute, 26 mm. long, the outer finely pubescent; filaments linear with minute triangular lobes, 16 mm. long, connate in a slender tube for most of their length; anthers affixed about $\frac{1}{3}$ above base, 10 mm. long; style slenderly clavate at apex.

Type in the Gray Herbarium of Harvard University, collected on rocks at edge of stream, sandstone area, Serra de Monjolo, 18 kilometers north of Sêro, Município of Sêro, State of Minas Gerais, Brazil, May 5, 1945, by Louis O. Williams and Vicente Assis (No. 6816).

53. **Barbacenia ensifolia** Mart. ex Schult. f. *in* R. & S. Syst. 7: 287. 1826.
BRAZIL: Minas Gerais: Serra da Lapa.
54. **Barbacenia glaziovii** Goeth. & Henr. Blumea 2: 348. 1937.
BRAZIL: Minas Gerais: Biribiri to Diamantina.
55. **Barbacenia conicostigma** Goeth. & Henr. Blumea 2: 341. 1937.
BRAZIL: Minas Gerais: Serra da Lapa.
56. **Barbacenia cuspidata** Goeth. & Henr. Blumea 2: 342, fig. C. 1937.
BRAZIL: Minas Gerais (?): No locality.
57. **Barbacenia longiflora** Mart. Nov. Gen. & Sp. 1: 19, pl. 12. 1823.
BRAZIL: Minas Gerais: Tejuco, near Diamantina. Guinda.
58. **Barbacenia gardneri** Seubert *in* Mart. Fl. Bras. 3, pt. 1: 70, pl. 8, fig. 5. 1847.
BRAZIL: Minas Gerais: Diamantina. Sêrro.
59. **Barbacenia curviflora** Goeth. & Henr. Blumea 2: 342. 1937.
BRAZIL: Minas Gerais: Rio das Pedras by Valu.
60. **Barbacenia fragrans** Goeth. & Henr. Blumea 2: 345. 1937.
BRAZIL: Minas Gerais: Caldas. São Paulo: São João da Boa Vista.
61. **Barbacenia tricolor** Mart. Nov. Gen. & Sp. 1: 18, pl. 10. 1823.
BRAZIL: Minas Gerais: Serra da Tiradentes. Serra de Rola Moca. Serra do Cipó.
62. **Barbacenia blanchetii** Goeth. & Henr. Blumea 2: 339. 1937.
BRAZIL: Bahia: "Igreja Velha." Jacobina. Pouço d'Areia.
63. **Barbacenia mollis** Goeth. & Henr. Blumea 2: 356. 1937.
- 63a. **Barbacenia mollis** var. **mollis**.

Leaf-blades to 12 cm. long, 12 mm. wide.

BRAZIL: Minas Gerais: No locality.

- 63b. **Barbacenia mollis** var. **microphylla** L. B. Smith, var. nov.

A var. *mollis* foliis multo minoribus differt.

Leaf-blades to 8 cm. long, 4 mm. wide; flower red (! Williams).

Type in the Gray Herbarium of Harvard University, collected on iron ore slope, Serra da Mutuca, beyond Barreiro, Município of Nova Lima, State of Minas Gerais, Brazil, altitude 1400 meters, April 15, 1945, by Louis O. Williams and Vicente Assis (No. 6641).

64. **Barbacenia leucopoda** L. B. Smith, sp. nov. PLATE 10, FIGURES 29, 30

A *B. damaziana* Beauverd, cui aliquid affinis, scapi indumento pallido, floribus minoribus differt.

Caudex about 6 cm. long; leaves densely imbricate; sheaths broadly ovate, 2 cm. long, glabrous, rather laxly nerved; blades linear-lanceolate, acute, 15 cm. long, 12 mm. wide at the middle, finely and densely setose-glandular; scape solitary, 9 cm. high above the leaf-bases, slender, densely vestite with fine white gland-tipped trichomes; flowers orange; perianth-tube subcylindric, very slightly enlarged upward, 25 mm. long, about 3 times as long as the ovary, very dark setose-glandular; tepals suberect at anthesis, elliptic, obtuse, 15 mm. long; filaments subtriangular, 7 mm. long, their appendages narrow, acute;

anthers linear, 9 mm. long, exceeding the filament-appendages by about $\frac{1}{3}$; stigmas small, apical, subcapitate.

Type in the herbarium of the University of California, No. 972105, collected in campo, Serra do Cipó, Município of Mato Dentro, State of Minas Gerais, Brazil, January 15, 1951, by Amaro Macedo (No. 2999).

65. *Barbacenia blackii* L. B. Smith, sp. nov.

PLATE 10, FIGURES 31, 32

A. B. damaziana Beauverd, cui affinis, filamentis oblongis antheris paulo superatis, foliis latioribus differt.

Caudex about 3 cm. long; leaves numerous, rather persistent, densely imbricate; sheaths broadly ovate, 1 cm. long, the lower half glabrous except the glandular-ciliate margins, narrowly sulcate, amplexicaul at base; blades linear-lanceolate, slightly narrowed toward base, cuspidate-acuminate, 10–13 cm. long, 9 mm. wide, finely and densely setose-glandular; scape solitary, 6–10 cm. long, less than 1 mm. in diameter, finely and densely setose-glandular; perianth-tube 3–4 cm. long, slightly constricted and subcylindric above the ellipsoid ovary and about 3 times as long, red, densely setose-glandular; tepals suberect at anthesis, elliptic-oblong, obtuse, 14–17 mm. long; filaments oblong with large lobes surpassing the centers of the anthers; anthers linear, 8 mm. long, extending only slightly below the filament-sinus.

Type in the U.S. National Herbarium, No. 2221524, collected on the Serra do Cipó, State of Minas Gerais, Brazil, January 13, 1951, by J. M. Pires and G. A. Black (No. 2734).

BRAZIL: Minas Gerais: Mun. Mato Dentro: In campo, alt. 1600 m., January 15, 1951, *A. Macedo* 2962 (US).

66. *Barbacenia rubra* L. B. Smith, sp. nov.

PLATE 10, FIGURES 33, 34

A. B. damaziana Beauverd, cui affinis, tepalis late rotundatis apiculatisque, filamentis oblongis, antheris subbasifixis basi filamentorum haud attingentibus differt.

Caudex unknown except for apex, this about 1 cm. in diameter (including leaf-sheaths); leaves densely imbricate; sheaths broadly ovate, ca. 15 mm. long, glabrous below the apex, sulcate, lustrous; blades very narrowly triangular, filiform-acuminate, 14 cm. long, 5 mm. wide, finely and densely setose-glandular; scape solitary 10 cm. long, very slender, setose-glandular; perianth-tube 35 mm. long, cylindric above the broadly obovoid ovary, 8 mm. in diameter, red (! Williams), densely setose-glandular; tepals erect at anthesis, oblong, broadly rounded and apiculate, 20 mm. long; filaments oblong with short lobes, 7 mm. long; anthers linear, 9 mm. long, subbasifixed, extending only slightly below the filament-sinus.

Type in the Gray Herbarium of Harvard University, collected on rocky slopes, Serra da Mutuca, Município of Nova Lima, State of Minas Gerais, Brazil, February 1945, by Louis O. Williams (No. 5432a).

67. *Barbacenia damaziana* Beauverd, Bull. Herb. Boiss. II. 5: 1078. 1905.
BRAZIL: Minas Gerais: Pico d'Itacolumi.

68. *Barbacenia bahiana* L. B. Smith, sp. nov. PLATE 10, FIGURES 35, 36

A *B. damaziana* Beauverd, cui affinis, ovario basi longe attenuato anguste obconico differt.

Caudex unknown except for apex, this about 7 mm. in diameter; leaves 3-ranked, densely imbricate; sheaths closely sulcate with the nerves almost contiguous; blades linear, attenuate to a filiform apex, 15 cm. long, 5–8 mm. wide, entire, sulcate on both sides, densely vestite with long acuminate setae and much shorter stipitate glands; scape solitary, extending 6 cm. above the leaf-sheaths, more glandular than the leaf-blades; perianth-tube 4 cm. long, subdensely pale glandular, slenderly cylindric above the ovary, 4 mm. in diameter; ovary slenderly obconic; tepals erect at anthesis, oblong, broadly subacute, 15 mm. long, 3 mm. wide, the outer minutely glandular, the inner nearly glabrous; stamens slightly shorter than the tepals, filaments subtriangular with broad base and short appendages; anthers linear, basifixed, 11 mm. long; style about equaling the tepals, broadly ovoid at apex with 3 ovate stigmas.

Type in the U.S. National Herbarium, No. 762256, collected in the vicinity of Machado Portello, State of Bahia, Brazil, June 19–23, 1915, by J. N. Rose and P. G. Russell (No. 19924).

Excluded and Doubtful Taxa

Barbacenia gracilis hort. ex Baker, Journ. Linn. Soc. 18: 239. 1880. Nomen.

This horticultural name was published in the synonymy of *Dasyli-
rion acrotrichum* Zucc., a liliaceous species of Mexico.

Vellozia coerulescens hort. Belg. ex Gumbel. Gard. Chron. for 1874. 2: 623, 657. 1874.

According to Jackson, Index Kewensis 4: 1173. 1895, this horticultural name is a synonym of *Barbacenia purpurea* Hook.

Vellozia duida Steyermark, Fieldiana Bot. 28, no. 1: 157. 1951.

The species is based on sterile material from southern Venezuela. It is related to if not identical with *V. tubiflora* (A. Rich.) H.B.K.

Vellozia hirsuta Goeth. & Henr. Blumea 2: 374. 1937.

This species was described from sterile material collected at Biri-biri, Minas Gerais, Brazil.

Vellozia lanata Pohl, Pl. Bras. 1: 130. 1827.

This species was described from sterile material collected at Caldas Novas, Goiás, Brazil.

Vellozia leptophylla Seubert in Mart. Fl. Bras. 3, pt. 1: 84. 1847.

This species was based on a sterile collection by Sellow without any indication of locality. Consequently there is not much hope of its ever being clarified.

Vellozia scabra Spreng. Syst. 3: 338. 1826.

The single line of description reads: "V. capsula glabra, scapo hispido," leaving little hope of ever identifying the species, although effecting valid publication.

Vellozia squamata auctt. ex Steud. Nom. Bot. ed. 2. 2: 746. 1841. Nomen.

This name was published in the synonymy of *Xerophyllum sabadilla*, a Mexican liliaceous species of doubtful identity. It is scarcely more than evidence of a misdetermination.

Vellozia tomentosa Pohl, Pl. Bras. 1: 130. 1827.

This species was described from sterile material collected between the crossing of the Rio Jequitinhonha and Calumbi, Minas Gerais, Brazil.

Vellozia triquetra Pohl, Pl. Bras. 1: 129. 1827.

This species was described from sterile material collected between Inhumas and Quartel do Teixeira, District of Minas Novas, Minas Gerais, Brazil.

Supplement

The following novelties were received too late to be included in the foregoing revision, but are correlated with it by species numbers. The Latin diagnosis gives the salient differences between each novelty proposed and its nearest relatives in the key.

3a. Vellozia maxillarioides L. B. Smith, sp. nov.

PLATE 11, FIGURE 37

A *V. abietina* Mart., cui affinis, ramis elongatis, vaginis foliorum lepidibus erectis fimbriatis praeditis, ovario angustissime sulcato differt.

Plant slender, branched, to 5 dm. high (! Maguire); branches ca. 4 mm. in diameter including the old leaf-bases; leaves few-ranked, laxly imbricate, the complete ones 2–5 at the apex of the branch; sheaths ca. 3 cm. long, tubular at base, very densely nerved, yellow-brown, subdensely vestite with erect white fimbriate scales; blades linear, abruptly acute and cuspidate, 4 cm. long, 3.5 mm. wide, densely nerved, lepidote on the thickened yellow margins, elsewhere glabrous, the keel somewhat prominent beneath; scape single, exactly equaling the leaf-sheath so that the flower appears sessile, soon lateral; capsule slenderly obconic, 10 mm. long, very densely and coarsely ribbed, otherwise even and glabrous.

Type in the U.S. National Herbarium, No. 2369002, collected on sandstone, slopes and summit of Grão Mogul, State of Minas Gerais, Brazil, altitude 900–1100 meters, August 17, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49268). Isotype in the New York Botanical Garden.

16a. *Vellozia fruticosa* L. B. Smith, sp. nov.

PLATE 11, FIGURES 38, 39

A *V. ambigua* Goeth. & Henr. et. *V. martiana* Goeth. & Henr., cuibus ex descriptionibus affinis, caudice graciliore, foliorum laminis glutinosis persistentibus, floribus multo minoribus differt.

Fruticose, much branched (! Maguire); caudex 7–8 mm. in diameter including old leaf-bases; leaves few-ranked, subdensely imbricate, the living about 5; sheaths ca. 2 cm. long, tubular at base, densely nerved except the narrow brown margin, glabrous, not dividing with age; blades linear, acute and long-cuspidate, 7 cm. long, 3 mm. wide, sparsely and minutely serrulate on the keel beneath, on the margins, and in two longitudinal lines above, the living very glutinous, erect to spreading, the dead reflexed and evidently persistent for several seasons; scape single, 7–8 cm. long, 0.8 mm. in diameter, nearly even, sparsely and obscurely glandular toward apex; stamens 18, appendaged at base; capsule ellipsoid, 8 mm. long, sharply trigonous with several additional costae, stipitate-glandular on the costae.

Type in the U.S. National Herbarium, No. 2368988, collected on sandstone outcrop, ca. 3–5 km. east of Serra, along road to Diamantina, State of Minas Gerais, Brazil, August 9, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49130). Isotype in the New York Botanical Garden.

26a. *Vellozia grao-mogulensis* L. B. Smith, sp. nov. PLATE 11, FIGURES 40–42

V. squalida Mart. ex Schult. f. in systema mea proxima sed habito caespitoso humile, foliis angustioribus densioribusque, scapo densiuscule stipitato-glanduloso differt.

Plant caespitose; caudex short, much branched, ca. 8 mm. in diameter including old leaf-bases; leaves rather many-ranked, very densely imbricate, the living ones only 4 or 5 at the apex of the branch; sheaths 17 mm. long, almost completely covered; blades linear, attenuate, to 9 cm. long, 1.8 mm. wide, densely pale-lepidote on both sides at first, the keel and thickened margins purple-black, the margins serrulate; scapes 1 or rarely 2, 12–15 cm. long, very slender, subdensely stipitate-glandular; ovary subglobose, 5 mm. in diameter, much enlarged in fruit, evenly and subdensely dark-glandular; tepals subequal, elliptic, obtuse, 17 mm. long, purple; stamens 18, appendaged at base, much shorter than the tepals.

Type in the U.S. National Herbarium, No. 2368996, collected on sandstone, Serra Grão Mogul, north base of mountain, State of Minas Gerais, Brazil, altitude 600–700 meters, August 16, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49218). Isotype in the New York Botanical Garden.

27a. *Vellozia bicolor* L. B. Smith, sp. nov.

PLATE 11, FIGURES 43–45

A *V. aloifolia* Mart., cui affinis, foliis bicoloribus, ovario grosse stipitato-glanduloso differt.

Plant 3–5 dm. high (! Maguire); caudex to 5 cm. in diameter (! Maguire); leaves many-ranked, very densely imbricate, the complete ones about 9 at the apex of the caudex; sheaths ample, 55 mm. long, densely nerved, white-lanate at apex, elsewhere glabrous, black with brown margins, lustrous; blades soon deciduous, linear, acuminate, 30–35 cm. long, 2 cm. wide, even, green, and glabrous above, completely cinereous-lanate beneath, the midnerve impressed above, prominent beneath; scapes 1–2, 25 cm. long, obtusely trigonous, 4 mm. wide, densely stipitate-glandular especially toward apex; tepals (only remnants known) glandular-appendaged at base; stamens about 40; capsule globose, 25 mm. in diameter, densely and coarsely stipitate-glandular.

Type in the U.S. National Herbarium, No. 2368976, collected on rocky sandy soil, summit of Serra do Cipó, road from Hotel Chapeu de Sol between Km. 111 and 120, State of Minas Gerais, Brazil, altitude 1200 meters, August 6, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49037). Isotype in the New York Botanical Garden. Same, No. 49047 (NY, US).

37a. *Vellozia mollis* L. B. Smith, sp. nov.

PLATE 11, FIGURES 46–48

A *V. resinosa* Mart. ex Schult f., cui affinis, foliis juvenilibus utrinque molliter denseque albo-tomentosis, ovario e glochidiis dimorphis dense glanduloso differt.

Caudex nearly 5 cm. in diameter including old leaf-bases; leaves many-ranked, very densely imbricate, the complete ones about 12; sheaths ample, 35 mm. long, densely nerved, dark castaneous, lustrous, the apical half densely white-tomentose; blades linear, acute to sub-obtuse, 13 cm. long, 8 mm. wide, at first densely white-tomentose, then becoming more or less glabrous and green above; scapes 1–2 (?), 22 cm. long, obtusely trigonous, densely stipitate-glandular toward apex; ovary subglobose, densely vestite with two types of glandular trichomes, one short and conical, the other about twice as long with a setose prolongation; stamens numerous; capsule 10 mm. long.

Type in the U.S. National Herbarium, No. 2368991, collected on sandstone outcrop, ca. 3–5 km. east of Serra, along road from Conceição to Diamantina, State of Minas Gerais, Brazil, August 9, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49156). Isotype in the New York Botanical Garden.

37b. *Vellozia spiralis* L. B. Smith, sp. nov.

PLATE 11, FIGURES 49–51

A *V. resinosa* Mart. ex Schult. f., cui affinis, vaginis foliorum apice ciliatis alibi glabris, laminis basi ciliatis alibi glabris differt.

Plant to 2.5 meters high (! Maguire), over 3 cm. in diameter including old leaf-bases; leaves few-ranked in a strong spiral, densely

imbricate, the complete ones about 20; sheaths ample, 4 cm. long, densely nerved and dark castaneous except for the thin pale margin, lustrous, disintegrating at apex and the whitish fibers recurving in a tight coil, coarsely setose-ciliate toward apex, elsewhere glabrous; blades linear, rounded and retuse, 30 cm. long, 11 mm. wide, setose-ciliate at extreme base, erect-serrulate on the margins, densely nerved, otherwise even and glabrous; scapes 3, 12–15 cm. long, 2.5 mm. in diameter, sulcate, densely and finely stipitate-glandular toward apex; ovary subglobose, 15 mm. long, subdensely and finely stipitate-glandular; tepals subequal, elliptic, 45 mm. long, purple; stamens ca. 40, the phalanges appendaged.

Type in the U.S. National Herbarium, No. 2369000, collected on sandstone, slopes and summit of Grão Mogul, State of Minas Gerais, Brazil, altitude 900–1100 meters, August 17, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49261). Isotype in the New York Botanical Garden.

38a. *Vellozia coronata* L. B. Smith, sp. nov.

PLATE 11, FIGURES 52–54

A *V. brevifolia* Seubert, cui affinis, habito subacaule, foliis floribusque majoribus, ovario tubo brevi coronato differt.

Caudex simple or forked, 4 cm. long; 3 cm. in diameter including the old leaf-bases; leaves very densely imbricate, the complete ones 4–5 at the top of the caudex; sheaths ample, 3 cm. long, dark castaneous, glabrous, lustrous, the old ones deeply divided; blades linear, narrowly obtuse and bicarinate near apex, to 16 cm. long, 15 mm. wide, very densely and finely serrulate-ciliate, otherwise glabrous and nearly even, the midnerve impressed on both sides; scapes at least 2, 9–15 cm. long, sulcate and subdensely stipitate-glandular toward apex; stamens 18 or more, appendaged at base; capsule subglobose, 12 mm. long, subdensely stipitate-glandular, crowned with a short epigynous tube.

Type in the U.S. National Herbarium, No. 2368985, collected on sandstone outcrop, ca. 20 km. from Conceição on the road from Conceição to Diamantina, State of Minas Gerais, Brazil, August 9, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49114). Isotype in the New York Botanical Garden.

39a. *Vellozia epidendroides* Mart. ex Schult. f. var. **major** L. B. Smith, var. nov.

A var. *epidendroides* habito majore, foliorum vaginis densiore imbricatis, laminis longioribus differt.

Plant 1.5 meters high (! Maguire); sheaths of the leaves ca. 3 cm. long, exserted less than 1 cm.; blades 12 cm. long.

Type in the U.S. National Herbarium, No. 2368982, collected on rock exposures, summit of Serra do Cipó, along road from Hotel Chapeu do Sol, km. 120–140, State of Minas Gerais, Brazil, altitude 1200–1300 meters, August 8, 1960, Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49098). Isotype in the New York Botanical Garden.

39b. *Vellozia epidendroides* Mart. ex Schult. f. var. *divaricata* L. B. Smith, var. nov.

A var. *epidendroides* habito ramosiore, ramis divaricatis brevibus, foliorum vaginis densiore imbricatis differt.

Plant 3 dm. high (! Maguire); branches 3–5 cm. long; sheaths of the leaves exerted for 5 mm.; blades to 8.5 cm. long.

Type in the New York Botanical Garden, collected on rocks, sandstone terraces and ridges, summit of Serra do Cipó, km. 112–128 along road from Hotel Chapeu de Sol, State of Minas Gerais, Brazil, altitude 1200–1300 meters, August 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49064).

39c. *Vellozia marcescens* L. B. Smith, sp. nov.

A *V. epidendroides* Mart. ex Schult. f., cui affinis, foliis marcescentibus, laminis reflexis persistentibus plus attenuatis, scapo brevior differt.

Caudex erect, slender, mostly covered by old leaves; leaves few-ranked; sheaths tubular, much exposed apically, very densely nerved, yellow-brown, glabrous, lustrous; blades linear, attenuate to a narrowly obtuse apex, closely nerved beneath, serrulate on the margins, otherwise even and glabrous, the living few, erect to spreading, the old blades reflexed, long-persistent; scapes 1–2, soon becoming lateral, slender, at first shorter than the leaves, densely stipitate-glandular toward apex; ovary subglobose, densely stipitate-glandular; tepals appendaged at base; stamens about 24.

Vellozia marcescens var. *marcescens*

PLATE 11, FIGURES 55–57

Planta fere omnibus partibus majoribus, caudice ramoso, scapis minoribus.

Caudex incompletely known but over 3 dm. high, branched, 5 mm. in diameter (including the old leaf-sheaths); leaf-blades to 7 cm. long, 7 mm. wide; scapes 15–20 mm. long above the leaf-sheaths.

Type in the U.S. National Herbarium, No. 2368998, collected on sandstone, slopes and summit of Serra Grão Mogul, Minas Gerais, Brazil, altitude 900–1100 meters, August 17, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49259). Isotype in the New York Botanical Garden.

Vellozia marcescens var. *minor* L. B. Smith, var. nov.

A var. *marcescente* caudice simplici, foliis minoribus, scapis majoribus differt.

Caudex simple, to 2 dm. high, 3 mm. in diameter including the old leaf-sheaths; leaf-blades to 45 mm. long, 3.5 mm. wide; scapes to 35 mm. long above the leaf-sheaths, evidently elongating in fruit.

Type in the U.S. National Herbarium, No. 2368997, collected on sandstone, Serra Grão Mogul, north base of mountain, altitude 600–700 meters, August 16,

1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49219). Isotype in the New York Botanical Garden.

42a. *Vellozia ciliata* L. B. Smith, sp. nov.

PLATE 11, FIGURES 58, 59

A *V. cryptantha* Seubert, cui affinis, laminis foliorum multo latioribus basi dense longeque ciliatis, ovario obscure verruculoso differt.

Caudex to 15 cm. long, 1-2-branched (! Maguire), 4-5 cm. in diameter including the leaf-bases; (! Maguire), the complete ones numerous; leaves many-ranked, very densely imbricate; sheaths broadly ovate, over 25 mm. long, very densely nerved with a thin nerveless margin, pale stramineous, glabrous, lustrous; blades linear, subacute and cuspidate, 20 cm. long, 10 mm. wide, densely ciliate toward base with long suberect yellow-brown setae, elsewhere glabrous, the midnerve impressed above, prominent beneath; scapes 1-2 (?), slenderly clavate, 2 cm. long; capsule obconic, truncate, 15 mm. long, stramineous, lustrous, obscurely verruculose, hidden by the leaves.

Type in the U.S. National Herbarium, No. 2368992, collected on sandstone outcrop ca. 3-5 km. east of Serra, along road from Conceição to Diamantina, State of Minas Gerais, Brazil, August 9, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49158). Isotype in the New York Botanical Garden.

62a. *Vellozia pulchra* L. B. Smith, sp. nov.

PLATE 12, FIGURES 60-62

A *V. cinerascens* Mart. ex Schult. f., cui verisimiliter affinis, foliis majoribus glabris, glochidiis ovarii apice subulato-acuminatis haud divisus differt.

Somewhat branched shrub about 1 meter high (! Maguire); caudex 2 cm. in diameter (including the old leaf-sheaths) near apex; leaves densely few-ranked; sheaths tubular at base, 3 cm. long, glabrous, yellow-brown with a narrow white margin where covered, lustrous, very densely nerved, remaining entire; blades many in the terminal fascicle, linear-lanceolate, retuse at apex, to 27 cm. long, 15 mm. wide, closely nerved, serrulate on the keel and margins, otherwise even and glabrous; scape single, 18 cm. long above the leaf-sheaths, even, glabrous; ovary broadly ellipsoid 15 mm. long, covered with suberect slender contorted pale subulate-acuminate trichomes; tepals subequal, elliptic-oblong, obtuse, 9 cm. long, 3 cm. wide, purple, finely pale-scabrous toward base; stamens 6; anthers linear, 3 cm. long.

Type in the U.S. National Herbarium, No. 2369003, collected on granite slopes immediately west of Pedra Azul, State of Minas Gerais, Brazil, August 21, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49289). Isotype in the New York Botanical Garden.

15a. *Barbacenia brevifolia* Taub. var. *recurvata* L. B. Smith, var. nov.

A var. *brevifolia* foliis recurvatis conduplicatis subduplo latioribus, floribus majoribus differt.

Leaf-blades arching-recurved, conduplicate, ca. 8 mm. wide; flowers 4 cm. long.

Type in the New York Botanical Garden, collected on rocks, Guinda, Município of Diamantina, State of Minas Gerais, Brazil, November 5, 1937, by H. L. Mello Barreto (No. 9526).

45a. *Barbacenia magalhaesii* L. B. Smith, sp. nov.

PLATE 12, FIGURES 63–65

A *B. gentianoides* Goeth. & Henr., cui valde affinis, foliis flores longe superantibus subtus glabris, floribus aureis minoribus differt.

Densely caespitose herb, branches seldom more than 10 cm. long (! Maguire); leaves numerous, persistent; sheaths ovate, 2 cm. long, amplexicaul, glabrous, sulcate; blades linear, filiform-acuminate, to 16 cm. long, 9 mm. wide, closely and finely nerved, glabrous beneath, subdensely glandular-tuberculate above, setose-ciliate on the narrow dark scarcely thickened margins; flowers appearing sessile, glabrous, yellow (! Maguire); perianth-tube slenderly cylindric, 4 cm. long, 3 mm. in diameter, flaring somewhat at apex; tepals suberect at anthesis, linear, broadly subacute, 3 cm. long; stamens 25 mm. long; filaments oblong with very short rounded lobes, high-connate; anthers attached near apex of filament, nearly basifixed, linear, 11 mm. long, purple; ovary slenderly ellipsoid, ca. 8 mm. long, nearly glabrous.

Type in the U.S. National Herbarium, No. 2368981, collected on sandstone rocks and ledges, road from Hotel Chapeu de Sol, Serra Cipó to Conceição, km. 120–140, State of Minas Gerais, Brazil, altitude 1200–1300 meters, August 8, 1960, by Bassett Maguire, Geraldo Mendes Magalhães and Celia K. Maguire (No. 49094). Isotype in the New York Botanical Garden.

BRAZIL: Minas Gerais: Mun. Jaboticatubas: Serra do Cipó, Conceição do Mato Dentro, Morro do Pilar, road to Pilar, October 16, 1953, F. Segadas Vianna & J. Lorêdo Jr. No. Serra-II-1066 (R, US). Frequent on rocks, sandstone terraces and ridges, summit of Serra do Cipó, km. 112–128 along road from Hotel Chapeu, alt. 1200–1300 m., August 7, 1960, *Maguire, Magalhães & Maguire* 49062 (NY).

45b. *Barbacenia sessiliflora* L. B. Smith, sp. nov. PLATE 12, FIGURES 66–68

A *B. gentianoides* Goeth. & Henr., cui parum affinis, foliis angustioribus, tubo perianthii angustissime obconici, filamentorum lobis triangularibus differt.

Plant only 5–10 cm. high but much branched; leaves numerous, persistent; sheaths broadly ovate, 7 mm. long, glabrous, sulcate; blades linear, acuminate, to 9 cm. long, 4 mm. wide, closely and finely nerved, glabrous except for the setose-ciliate margins; flowers sessile, red (! Magalhães); perianth-tube 5 cm. long, very slenderly obconic above the ovary, 5 mm. in diameter at apex, sparsely vestite with fine eglandular trichomes; tepals spreading at anthesis, nearly

uniform, oblong, 15 mm. long; filaments oblong, 4.5 mm. long, the lobes triangular, acuminate; anthers linear, exceeding the filaments by 5 mm.; ovary obovoid, 10 mm. long.

Type in the New York Botanical Garden, collected on rock, Serra Cata Altas, Município of Santa Barbara, State of Minas Gerais, Brazil, February 2, 1943, by Geraldo Mendes Magalhães (No. 6400). Cotype: Same data as the type, *Magalhães* 6854 (NY).

55a. *Barbacenia albiflora* L. B. Smith, sp. nov. PLATE 12, FIGURES 69, 70

A *B. conicostigma* Goeth. & Henr., cui valde affinis, foliis utrinque pilis glandulosis biformibus vestitis, floribus albis differt.

Stem short with multiple crown, very viscid (! Maguire); leaves numerous, persistent; sheaths ovate, over 3 cm. long, closely and finely nerved, glabrous; blades linear, filiform-acuminate, ca. 30 cm. long, 15 mm. wide, flat, laxly and coarsely setose and densely and minutely glandular on both sides, the keel and margins inconspicuous; scapes 3 or more, ca. 50 cm. long, much exceeding the leaves, coarsely and finely glandular intermixed especially toward apex; flowers white (! Maguire); perianth-tube 4 cm. long, slenderly cylindric and laxly and coarsely glandular above the ovary, densely and finely glandular on the ovary; tepals irregularly reflexed at anthesis, 2 cm. long, strongly dimorphic, the outer narrowly oblong, densely glandular, the inner elliptic, glabrous; filaments oblong, 8 mm. long, the lobes short, acuminate; anthers linear, 18 mm. long, extending below the base of the filament; ovary ellipsoid, 15 mm. long.

Type in the U.S. National Herbarium, No. 2368995, collected on sandstone, Serra Grão Mogul, north base of mountain, State of Minas Gerais, Brazil, altitude 600–700 meters, August 16, 1960, by Bassett Maguire, Geraldo Mendes Magalhães, and Celia K. Maguire (No. 49213). Isotype in the New York Botanical Garden.



Vellozia alata L. B. Smith (Maguire & Pires 44690).



FLORA OF BRAZIL
NEW YORK BOTANICAL GARDEN
EX HERB. BRIT. MUSEUM

Vellozia

U. S. NAT. HERB. JAN 1944 1936 1945 No. 5233

Vellozia streptophylla L. B. Smith (Gardner 5233).



Vellozia froesii L. B. Smith (Fróes 19980).



90914

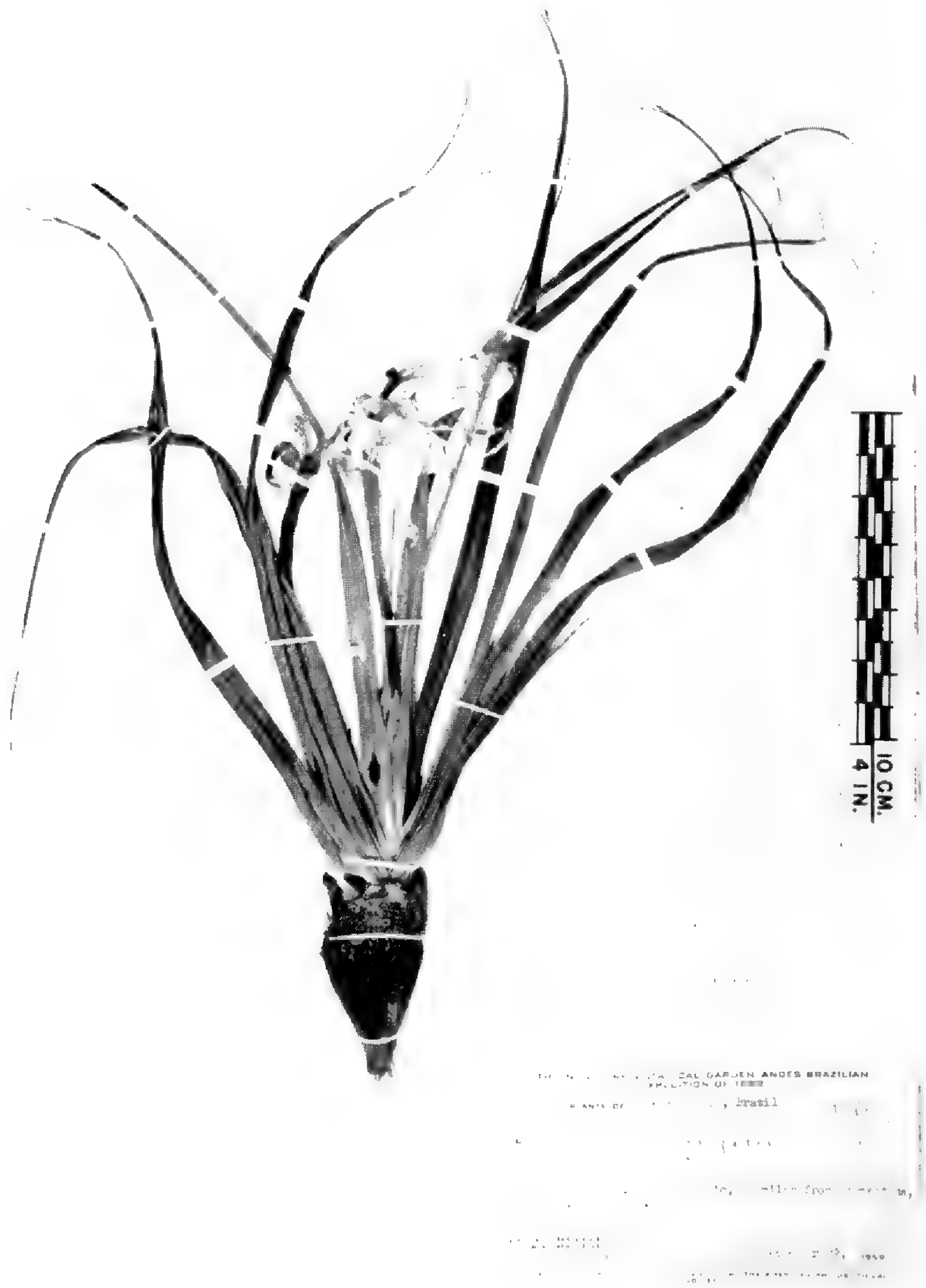
INSTITUTO A. GOV. DO NORTE
PLANTAS DA AMAZONIA
Estado do Pará

Vellozia

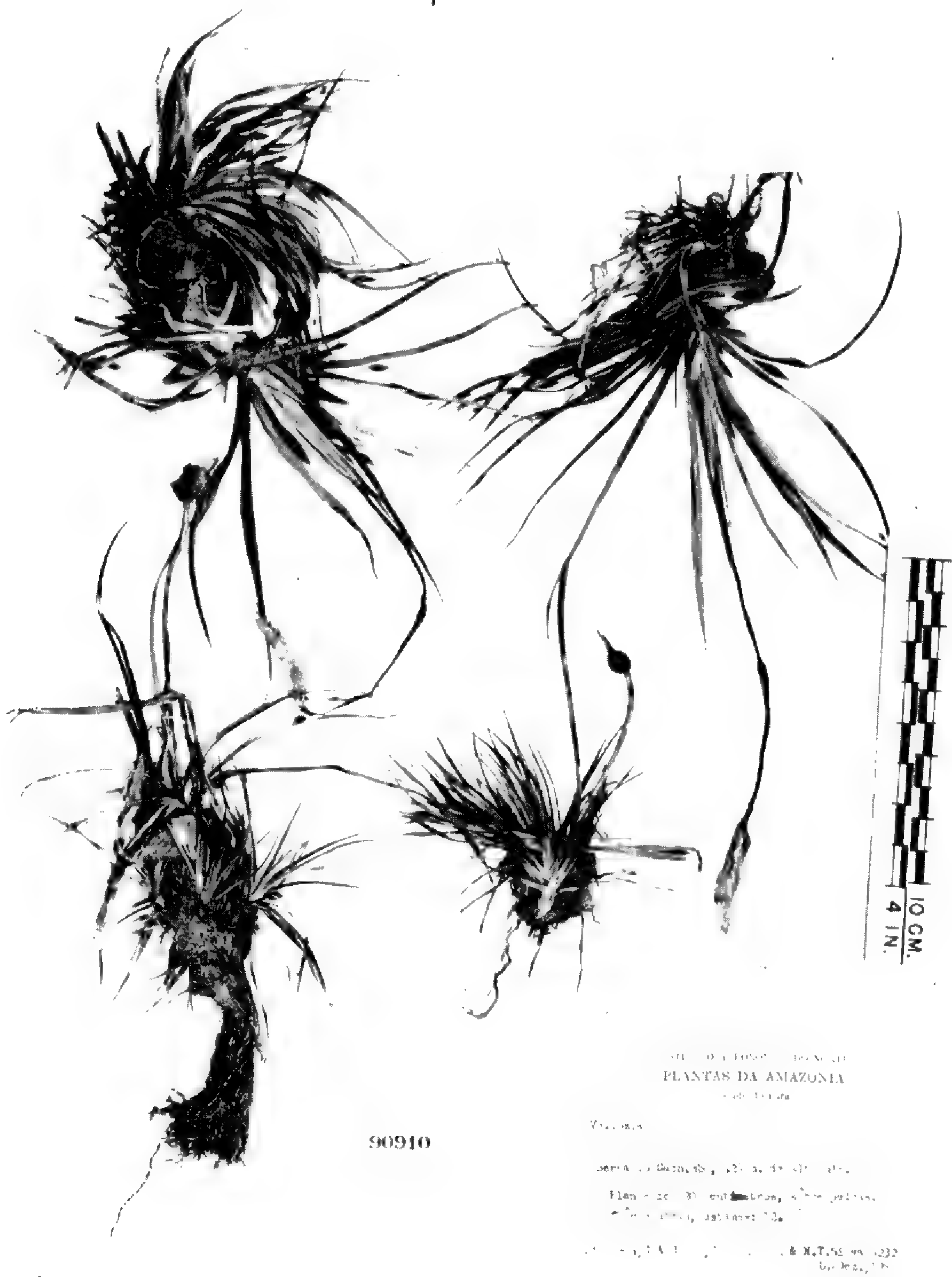
Serra do Cachimbo, 425 m. de altitude.
Planta baixa, flor branco-violeta
(orquidacea); em savana sobre pedras.

J.M.Pires, O.A. Black, J.J. Wurdack &
N.T. Silva 6423 19-Dez., 1956

Vellozia bulbosa L. B. Smith (*Pires et al.* 6423).



Vellozia maguirei L. B. Smith (Maguire & Pires 44742).



Vellozia cachimbensis L. B. Smith (*Pires et al.* 6232).



U. S. NATIONAL HERBARIUM
Dawson L. B. Smith

FLORA OF GOIAS, BRAZIL
Los Angeles County Museum
MACHRIS BRAZILIAN EXPEDITION

Region of the Canga de Vespasius at
W. Long. 47° 50', S. Lat. 14° 30'
sandstone outcrop 7 km. south of Vespasius

L. B. Dawson No. 14580 April 24th 1956

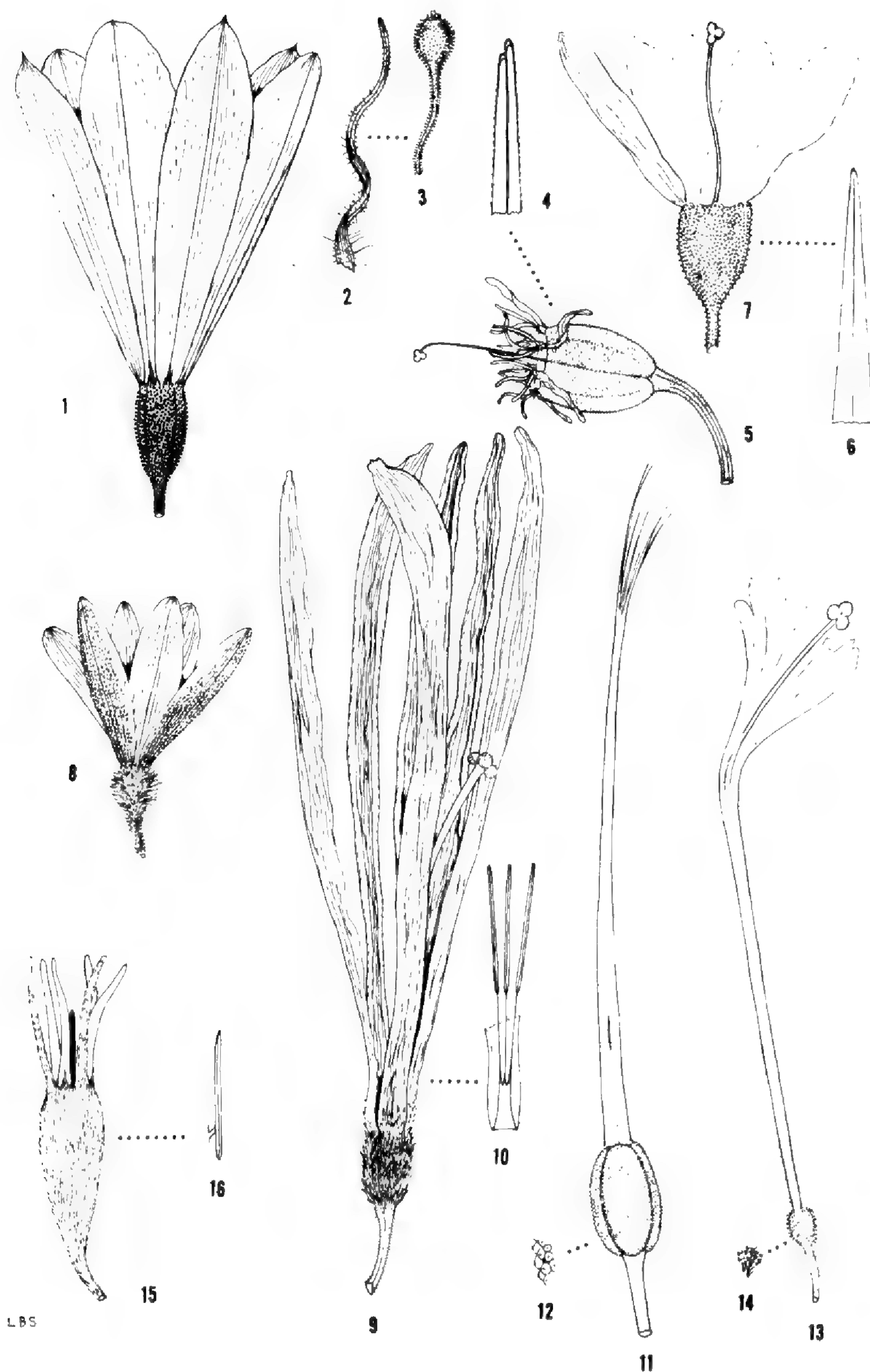
Vellozia dawsonii L. B. Smith (*Dawson* 14580).



THE NEW YORK BOTANICAL GARDEN
EXPLORATION OF THE
PLANTS OF THE

NEW YORK
BOTANICAL
GARDEN

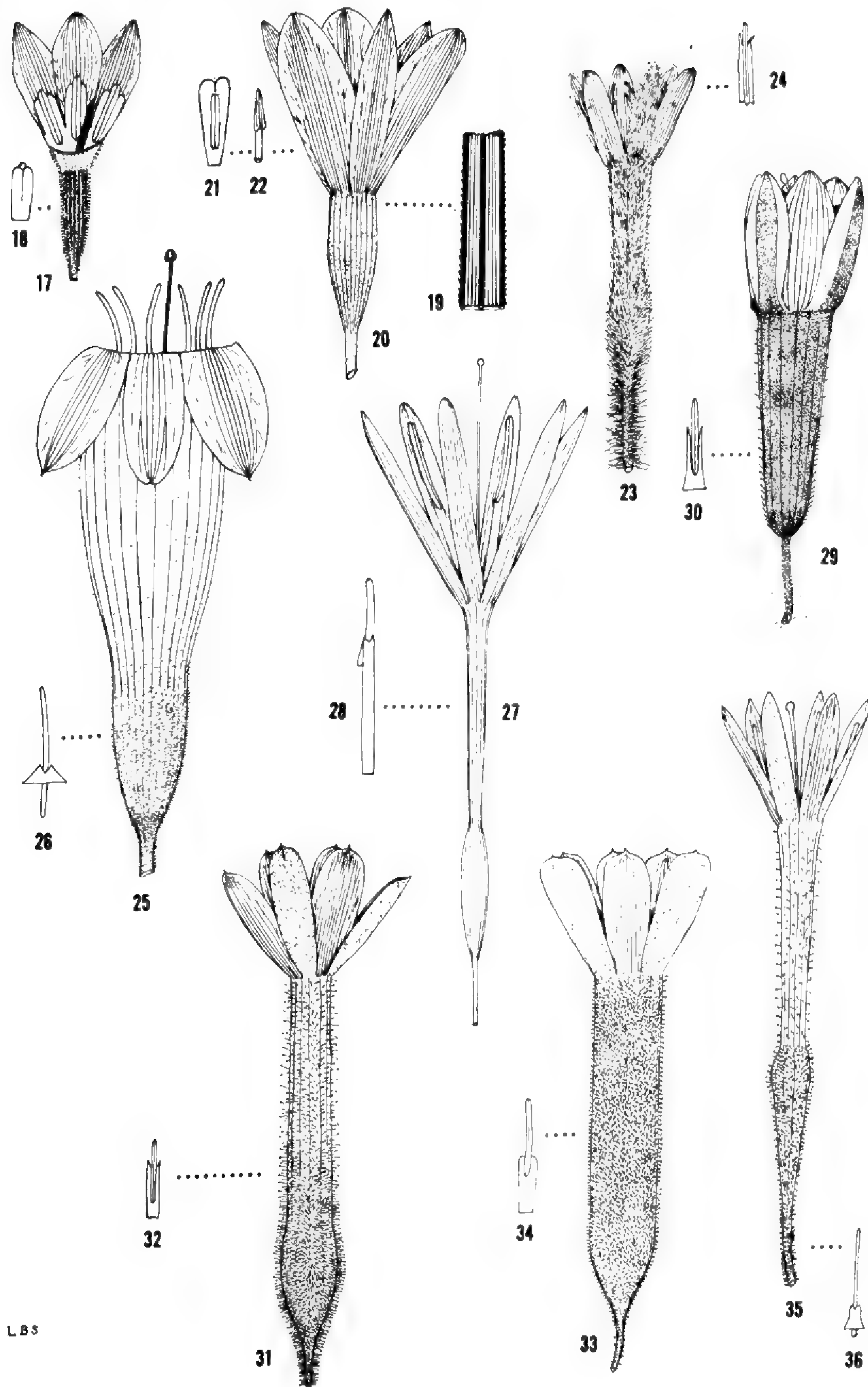
Barbacenia grisea L. B. Smith (Maguire & Pires 44745).



FIGURES 1-16.—(All figures $\times 1$, except 12 and 14 which are about $\times 5$): 1, *Vellozia viannae* L. B. Smith (*Segadas-Vianna* No. Serra II-1103), flower. 2, *V. streptophylla* L. B. Smith (*Gardner* 5233), leaf-blade; 3, fruit. 4, *V. ramosissima* L. B. Smith (*Maguire & Pires* 44666), apex of leaf-blade; 5, fruit. 6, *V. piresiana* L. B. Smith (*Black & Pires* 51-12157), apex of leaf-blade; 7, fruit. 8, *V. hypoxoides* L. B. Smith (*Macedo* 4330), flower. 9, *V. swallenii* L. B. Smith (*Swallen* 3617), flower; 10, phalange of stamens, ventral. 11, *V. machrisiana* L. B. Smith (*Dawson* 14674), fruit; 12, trichomes of ovary. 13, *V. uleana* L. B. Smith (*Ule* 8372), flower; 14, trichomes of ovary. 15, *Barbaceniopsis boliviensis* (Baker) L. B. Smith, fruit (*Schreiter* 2561); 16, stamen, lateral (*Bang* 1134).

SPECIES OF BARBACENIA

FIGURES 17-36.—(All figures $\times 1$): 17, *Barbacenia irwiniana* L. B. Smith (*Irwin* 2803), flower with tepals cut away; 18, stamen, dorsal. 19, *B. nigrimarginata*, L. B. Smith (*Dawson* 14717), section of leaf-blade; 20, flower; 21, stamen, ventral; 22, apex of style. 23, *B. williamsii* L. B. Smith (*Williams* & *Assis* 6696), flower; 24, stamen, ventral. 25, *B. paranaensis* L. B. Smith (*Hatschbach* & *Lange* 5359), flower; 26, stamen, dorsal. 27, *B. graciliflora* L. B. Smith (*Williams* & *Assis* 6816), flower; 28, stamen, dorsal. 29, *B. leucopoda* L. B. Smith (*Macedo* 2999), flower; 30, stamen, ventral. 31, *B. blackii* L. B. Smith (*Pires* & *Black* 2734), flower; 32, stamen, ventral. 33, *B. rubra* L. B. Smith (*Williams* 5432a), flower; 34, stamen, ventral. 35, *B. bahiana* L. B. Smith (*Rose* & *Russell* 19924), flower; 36, stamen, dorsal.

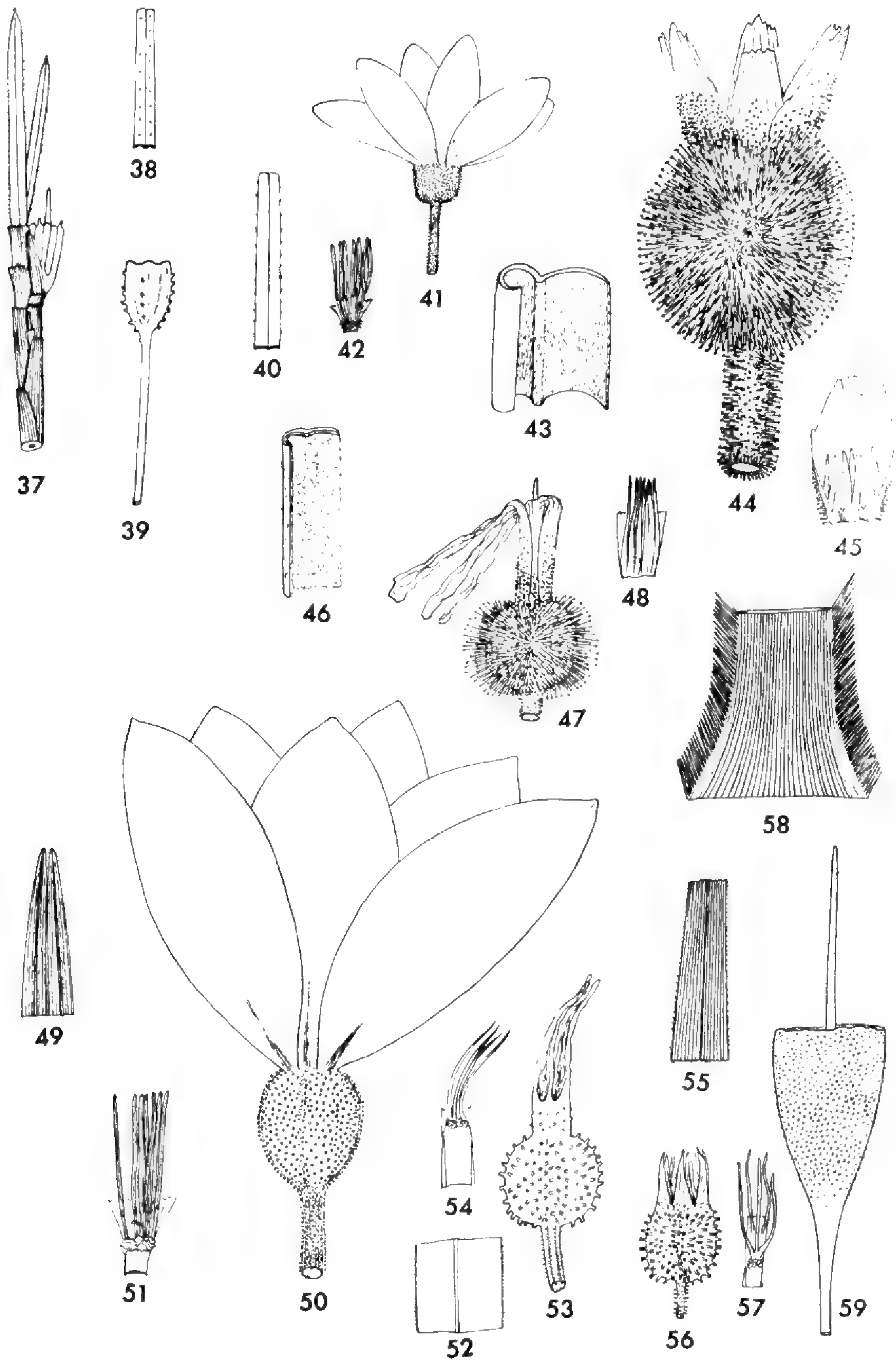


LBS

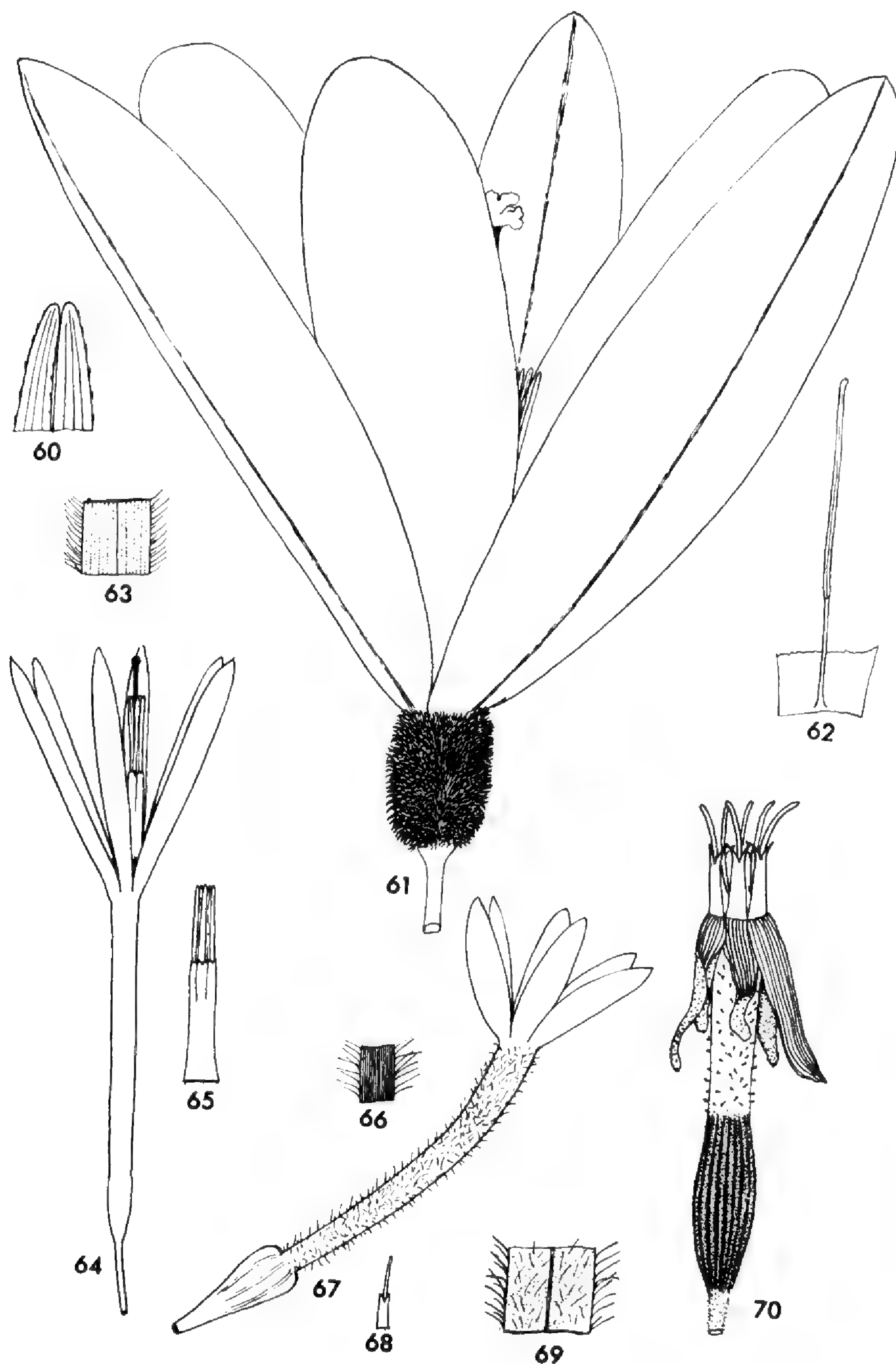
(For explanation see opposite page)

SPECIES OF VELLOZIA

FIGURES 37–59.—(All figures $\times 1$): 37, *Vellozia maxillarioides* L. B. Smith (*Maguire, Magalhães & Maguire* 49268), apex of branch. 38, *V. fruticosa* L. B. Smith (*Maguire, Magalhães & Maguire* 49130), section of leaf-blade; 39, capsule. 40, *V. grao-mogulensis* L. B. Smith (*Maguire, Magalhães & Maguire* 49218), section of leaf-blade; 41, flower; 42, phalange of stamens. 43, *V. bicolor* L. B. Smith (*Maguire, Magalhães & Maguire* 49037), section of leaf-blade; 44, capsule; 45, phalange of stamens (remnant). 46, *V. mollis* L. B. Smith (*Maguire, Magalhães & Maguire* 49156), section of leaf-blade; 47, capsule; 48, phalange of stamens (remnant). 49, *V. spiralis* L. B. Smith (*Maguire, Magalhães & Maguire* 49261), apex of leaf-blade; 50, flower; 51, phalange of stamens. 52, *V. coronata* L. B. Smith (*Maguire, Magalhães & Maguire* 49114), section of leaf-blade; 53, capsule; 54, phalange of stamens (remnant). 55, *V. marcescens* L. B. Smith var. *marcescens* (*Maguire, Magalhães & Maguire* 49259), section of leaf-blade; 56, capsule; 57, phalange of stamens (remnant). 58, *V. ciliata* L. B. Smith (*Maguire, Magalhães & Maguire* 49158), section of leaf at junction of blade and sheath; 59, scape and capsule.



(For explanation see opposite page)



FIGURES 60-70.—(All figures $\times 1$): 60, *Vellozia pulchra* L. B. Smith (Maguire, Magalhães & Maguire 49289), apex of leaf-blade; 61, flower; 62, stamen. 63, *Barbacenia magalhaesii* L. B. Smith (Maguire, Magalhães & Maguire 49094), section of leaf-blade; 64, flower; 65, stamens. 66, *B. sessiliflora* L. B. Smith (Magalhães 6400), section of leaf-blade; 67, flower; 68, stamen. 69, *B. albiflora* L. B. Smith (Maguire, Magalhães & Maguire 49213), section of leaf-blade; 70, flower

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(Synonyms are in *Italics*.)

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U N I T E D S T A T E S N A T I O N A L M U S E U M

CONTRIBUTIONS FROM THE UNITED STATES NATIONAL HERBARIUM

VOLUME 35, PART 5

SYNOPSIS OF
THE SOUTH AMERICAN SPECIES OF
VISMIA (GUTTIFERAE)

By JOSEPH EWAN



BULLETIN OF THE UNITED STATES NATIONAL MUSEUM
SMITHSONIAN INSTITUTION • WASHINGTON, D.C. • 1962

SYNOPSIS OF THE SOUTH AMERICAN SPECIES OF VISMIA (GUTTIFERAE)

JOSEPH EWAN

Introduction

Vismias are mostly low, leafy-crowned trees or tall shrubs, with opposite, broad, poplar-like leaves, and white, green, yellowish or brownish flowers borne in more or less crowded panicles. The flowers recall those of the genus *Hypericum*, the St.-John's-worts, and, indeed, Vismias were first described as species of *Hypericum*. The petals are usually hairy or even woolly, but the amount of hairiness varies in many instances among individuals of the same species. The usually black berry of *Vismia*, subtended by a rather prominent calyx, early attracted attention and provides a ready means of distinguishing this genus from *Hypericum*, with which it agrees in most technical characters, but which has a dry capsular fruit.

The first Vismias described were based on collections originating in Brazil and the Guianas. About four-fifths of the species of the genus are confined to tropical South America and these constitute the subject of the present synopsis. The few *Vismia* species known from Central America have been reviewed in connection with this study; they are mostly referred to the South American species but present some special problems. The only species from Mexico and Central America not otherwise mentioned in this treatment are *V. mexicana* Schlecht. and *V. camparaguay* Sprague. *Vismia* demonstrates Afro-American relationships, spanning as it does the South Atlantic Ocean, with five or six species occupying tropical West Africa, and one species isolated in the Pugu Range and near Dar es Salam on the coast of East Africa. Adolph Engler, in the last summary of the genus as a whole (1925), recognized about 30 species of *Vismia* but in all probability there are in the genus between 45 and 50 species. Knowledge of the ecological relationships and life histories is scanty but there are data that some species are giant forest trees whereas others are

characteristically early invading "weedy" species in disturbed vegetation and do not usually attain true tree stature.

The present study was undertaken in 1946 at the suggestion of Mr. E. P. Killip of the United States National Museum, while I was a member of the Museum staff, and his continuing interest in the problem and the placing of supplementary collections in my hands for study are appreciated. Work on the study was considerably advanced during the summer of 1947 by a grant from the Smithsonian Institution. Since then Dr. Elbert Little, Jr., and Dr. Richard Evans Schultes have made their Colombian collections available. The kindness of Mr. N. Y. Sandwith in checking types at Kew early in the progress of this study was particularly valuable. P. J. Eyma's careful notes on the types in European herbaria were often useful. The photographs of type specimens preserved in European herbaria made by Dr. J. Francis Macbride under the Rockefeller Foundation, together with fragments of authentic material now filed at the Chicago Museum of Natural History, have been of decisive importance in several instances. The use of three of these photographs to illustrate this paper is an appreciated privilege. Opportunity to examine the *Vismia* collections in person in European herbaria presented itself in 1954-55 when as a Guggenheim Fellow I visited 15 different institutions primarily for the study of archive materials bearing on the early botanical contacts between America and Europe. I am indeed grateful to the John Simon Guggenheim Memorial Foundation for this opportunity. The only important *Vismia* series not seen was that of Martius in the Botanische Staatssammlung, München, but duplicates of most of these were examined at Vienna and Paris.

It is a pleasure to acknowledge my indebtedness to several curators of herbaria in this country and abroad for making their series of *Vismias* available to me: Arnold Arboretum, Cambridge, Mass., (A); British Museum (Natural History), (BM); Academy of Sciences, San Francisco, Calif., (CAS); Botany School, Cambridge University, (CGE); Herbario Nacional Colombiano, Bogotá, (COL); Botanical Museum and Herbarium, Copenhagen, (C); Dudley Herbarium, Stanford University, (DS); The Royal Botanic Garden, Edinburgh, (E); Chicago Museum of Natural History, formerly the Field Museum, (F); Herbarium Universitatis Florentinae, Florence, (FI); Conservatoire et Jardin Botanique, Geneva, (G); Herbar de Candolle, Geneva, (G-DC); Dept. of Botany, Glasgow University, (GL); The Herbarium, Kew, (K); Rijksherbarium, Leiden, (L); Missouri Botanical Garden, (MO); National Arboretum Herbarium, Beltsville, Md., (NA);

Tulane University, New Orleans, (NO); Fielding Herbarium, Oxford University (OXF); Muséum National d'Histoire Naturelle, Paris, (P); Academy of Natural Sciences of Philadelphia, (PH); Naturhistoriska Riksmuseum, Stockholm, (S); Trinity College, Dublin, (TCD); Botanical Museum and Herbarium, Utrecht, (U); University of California, Berkeley, (UC); United States National Herbarium, (US); Naturhistorisches Museum, Vienna, (W); and Botanisches Institut and Botanisches Garten der Universität, Vienna, (WU).

The citation of abbreviations following the citation of specimens indicates that specimens have been studied by the writer in the herbaria concerned. The few specimens cited without such abbreviations, mostly types, have not been seen.

Finally, I am sincerely grateful to C. V. Morton for a careful scrutiny of this paper in editing it for publication.

TAXONOMIC HISTORY

The genus *Vismia* was established by Domingos Vandelli, Professor in Lisbon, in a small quarto volume entitled "Florae lusitanicae et brasiliensis specimen," published in Coimbra, Portugal, in 1788. Prof. Vandelli was first director of the Jardim Botânico da Universidade, Coimbra, from its founding in 1772 (or 1773?) until 1791. He was succeeded by the better known botanist Felix de Avellar Brotero (1744–1828), whose name is commemorated in the name of the Coimbra garden's bulletin, *Broteroa*. An examination of a copy of Vandelli's work (1788), in the Arnold Arboretum Library, shows that the re-publication of this rare volume by J. J. Roemer (Scriptores, pp. 67–164. 1796) is a *verbatim* textual copy and, as such, completely reliable. The original generic description of *Vismia* appears in Vandelli (1788) as shown in plate 1.

The illustration of the flower only, in his figure 24 which accompanies the original description, shows the petals about equal to the sepals, obovate, spotted, and ciliate all around. The illustration clearly fixes the generic identity of the plant Vandelli had before him, but its specific identity can hardly be determined because of its too generalized nature.

Vismia comprises the baccate-fruited species of *Hypericum*, including *Hypericum bacciferum*, mentioned in 1648 in Georg Marcgrav's *Historia naturalis Brasiliae*¹ (p. 96). In 1760 Jacquin proposed *Hypericum cayennense*, based on plants from French Guiana. In

¹ Published posthumously in a separately paged folio work by Willem Piso.

1775 Aublet described three additional species from French Guiana, *H. sessilifolium*, *H. latifolium* and *H. guianense*. J. B. C. Frisec Aublet (1720–1778) arrived in Cayenne on July 23, 1762, and remained two years collecting plants of the country as he had done during his previous nine-year sojourn in Mauritius. What is generally believed to be Aublet's principal herbarium is preserved at the British Museum (Natural History) and the *Vismias* contained therein have been studied by N. Y. Sandwith. A small collection of Aublet's uncovered at Carignan (Ardennes), France, apparently does not contain any *Vismia* types.²

In 1764 the elder Linnaeus³ published *Hypericum petiolatum*; it was credited to Brazil, but without citation of earlier references. Reichardt, who wrote the notable account of the genus for the *Flora Brasiliensis*,⁴ was unable to place *Hypericum petiolatum* L. *Hypericum petiolatum* L. is quite a different species, moreover, from the *H. petiolatum* of Linnaeus the Younger,⁵ a species based upon a collection, communicated by Mutis, which without doubt originated in Colombia. Authentic Mutis material is preserved in the United States National Herbarium and was studied in the preparation of this synopsis. *Hypericum petiolatum* L.f. is a homonym, however, and therefore not available for this Colombian species, which must be called *Vismia lauriformis* (Lam.) Choisy. A little later (1790), Loureiro used the name *Hypericum petiolatum* for the third time, quite independently and without any reference to the two separate uses of the name by Linnaeus, father and son, and he thus created a third homonym.⁶ Choisy was justifiably in doubt that Loureiro's name for a plant of southeast Asia concerned the Brazilian *Vismia* previously described as *Hypericum petiolatum* L. Merrill, in his "commentary" upon the binomials of Loureiro,⁷ refers *Hypericum petiolatum* Lour. to *Cratogeomys ligustrinum* (Spach) Blume (Guttiferae), as a synonym. In 1797 Lamarck added two more species to the genus under the generic name *Hypericum*, *H. rufescens* and *H. acuminatum*. In 1797 Ruiz and Pavon adopted the name *Vismia* and established two Peruvian species under that name, *V. glabra* and *V. tomentosa*.

² J. Lanjouw and H. Ulftien, Rec. trav. bot. neerl. 37 1: 133–170. 4 pls. 1940.

³ Sp. Pl. ed. 3. 1102. 1764.

⁴ 12 1: 210. 1878.

⁵ Supplementum 345. 1781.

⁶ Fl. Cochinch. 472. 1790 (Willd. reprint 577. 1793).

⁷ Amer. Philos. Soc. Trans. 24 2: 268. 1935.

Subsequent to 1800, additions to *Vismia* were made, either as transfers from *Hypericum* or as proposals under the name *Vismia*, by the following 23 botanists:

Persoon (1807)	Sagot (1880)
Poiret (1813)	Hieronymus (1895)
Choisy (1821)	Ruhland (1901)
Humboldt, Bonpland, and Kunth ⁸	Huber (1901, 1906)
(1822)	Sprague (1905)
St. Hilaire (1827)	Rusby (1912)
Schlechtendal and Chamisso (1828)	Blake (1918)
Martius (1828)	Hochreutiner (1919)
Miquel (1844, 1851)	Engler (1925)
Triana and Planchon (1862)	Ducke (1939)
Turczaninow (1863)	A. C. Smith (1939)
Reichardt (1878)	Cuatrecasas (1946)

Jacques Denys Choisy, son of a minister in Geneva, studied under Augustus Pyramus de Candolle and prepared a thesis entitled "Prodromus d'une monographie de la famille des Hypericineés," which was published in Geneva in 1821. The presentation copy to his master, now in the Conservatoire Botanique library, contains a letter from Choisy dated "1 Jan^r 1821," which would indicate that the "little work," as Choisy called it, was actually printed in 1820.

Engler summarized the genus in the second edition of Engler and Prantl's *Die natürlichen Pflanzenfamilien*,⁹ recognizing at that time the two sections in the genus founded by Reichardt in 1878, *Trianthera* and *Euvismia* (including *Stictopetalum*). N. Y. Sandwith, in his studies of the British Guiana flora,¹⁰ revived Miquel's name *Vismia angusta* for a species that was up to that time confused with either *Vismia latifolia* (Aubl.) Choisy or *V. macrophylla* H. B. K. Pierre Joseph Eyma, a student of Prof. A. Pulle, critically reviewed the Caribbean South American *Vismias* in the course of his doctoral thesis at the University of Utrecht.¹¹

British, French, and American botanists have remarked upon the need for realignment in the genus *Vismia*. A representative comment is that of L. A. M. Riley who has said that since "many of the old species [are] imperfectly known or misunderstood," the genus is in

⁸ Kunth wrote the botanical text of the *Nov. Gen. et Sp.* and perhaps should carry the credit alone, but for bibliographic purposes and in accordance with historical tradition it is desirable to use the well-established designation "H. B. K."

⁹ 21:185. 1925.

¹⁰ Kew Bull. 1931:174. 1931.

¹¹ *Polygonaceae, Guttiferae, and Lecythidaceae of Surinam*. 1932. cf. pp. 48-53. Reprinted in *Meded. Bot. Mus. & Herb. Utrecht* 4: 41-46. 1932. His tragic death is related by C. G. G. J. Van Steenis in *Bull. Bot. Gard. Buitenzorg*, ser. III, 18: 403-406. portr. 1950.

"urgent need of revision."¹² Sagot made in effect the same comment in 1880, and S. F. Blake wrote in 1918 that "the genus as a whole . . . is rather badly in need of a thorough revision."¹³

Though Adanson's characterization of the genus as *Caopia* in 1763 is clear and unmistakable, founded as it is on the references to Brazilian species in the works of Piso and Marcgrav, the generic name *Vismia* has been admitted to the Nomina Generica Conservanda of the International Code of Botanical Nomenclature, over the prior name *Caopia* of Adanson. *Vismia cayennensis* (Jacq.) Pers. was designated as the type species.

ECONOMIC USES

Vismia as a genus has no known commercial uses as a timber tree, since the boles are generally too small for lumber or of too poor quality for cabinet woods. However, some individuals of *Vismias* in Brazilian Amazonia attain a height of 25 meters. Among the Andean peasant farmers the genus is familiar as a conspicuous member of the second-growth woodland or along the borders of cleared land, where it may serve as an important species in erosion control because of its quick growth. It is also a tree of the lowland selva and occasional in the mountain rain forest. In both of these sites the trees flower more inconspicuously and lack the rather large panicles of bloom characteristic of trees growing in the open potreros. Certainly the large number of vernacular names for the genus attest to the familiarity of the trees among the natives over its wide range. Some of these folk names refer to the characteristic yellow or orange resinous sap which exudes rather freely from the cut stem. This resin is used in local folk medicines. The juice of the bark of *Vismia baccifera* is used in Boyacá, Colombia, by the Indians there to paint their faces (*teste* A. E. Lawrance). *Vismias* having the same vernacular name may be used for different purposes in different but adjacent regions. Thus, "swinani" was reported to be used as a fish poison by Pichoto, a Carib native, near Paramaribo, in November 1934 (W. A. Archer, Ms. report, p. 377, in files of U.S. Agricultural Research Service), whereas at Carolina, Surinam, "swinani" is not used as a fish poison but as a medicine (Dec. 16, 1934, W. A. Archer report). Perhaps it may be found that two different species of *Vismia* are involved here under the name "swinani." The bark of the *Vismia* is scraped and the juice used to cure "lota," a skin disease which Archer suggests may be of a fungal origin. Rudolf Graves, a gardener of Paramaribo, Surinam, reported to Archer that "pina" was used as a fish poison there, the bark being scraped into the water. The orange

¹² Kew Bull. 1925:134. 1925.

¹³ Contrib. Gray Herb. 53:42. 1918.

POLYADELPHIA.

— *aurantinum* * *Larangei-
ra*.

Vis. *fruct.* Corrobo-
rans, anthelmintica,
pellens.

POLYANDRIA.

VISMIA. Fig. 24.

CAL. Per. coriaceum, mo-
nophyllum, inferum, 5-
partitum, persistens,
foliolis ovato-acutis,
concavis.

COR. Petala 5, ovata,
intus pilosa.

STAM. filamenta plura in
5 phalanges s: corpora
connata, brevia, plana
incurva, apice multifida,
filamentis capillaribus,

villosis: *Antheræ* pluri-
mae, subrotundae facie
externa filamenti spi-
rae instar dispositae, s:
secundae.

Nectaria corpuscula s:
Glandulae 5. ovatae, pi-
losae inter phalanges.

PIST. Germen subrotun-
dum. *Styli* 5. filiformes.

Stigmata peltata.

PER. Capsula 5-locularis,
pentagona.

SEM. plurima. B.

Hypericum androsaemum.

— *quadrangulare*.

— *perforatum*. *Iperica* ð.

Vis. vulneraria, resol-
vens, anthelmintica.

— *humifusum*.

— *crispum*.

— *montanum*.



Vismia macrophylla
HBK. V. p. 142

growing in the forest

at

VISMIA MACROPHYLLA H. B. K.



Vismia parviflora Schlecht. & Cham.
Cuba: Matanzas.

Sept. 1907. Dr. J. M. S. S. S. S. S.

Typus!

VISMIA PARVIFLORA SCHLECHT. AND CHAM.



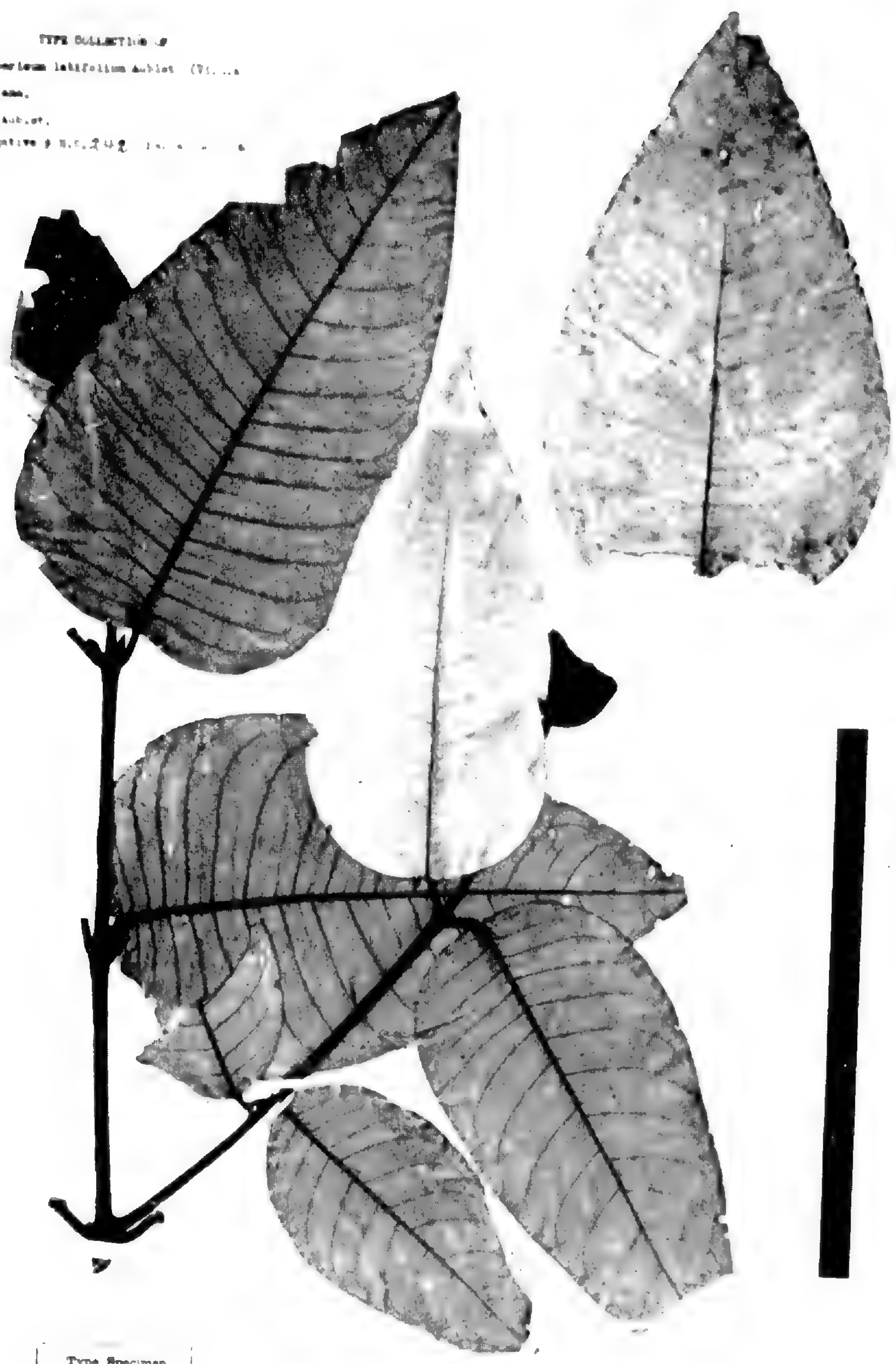
VISMIA RUFESCENS (LAM.) PERS. (=PETIOLATE FORM OF V. SESSILIFOLIA)

TYPE COLLECTION OF
Vismia sessilifolia Aublet (Vismia)
No. 1
Col. 1
No. 1, 1844



VISMIA SESSILIFOLIA (AUBL.) DC.

TYPE COLLECTION OF
Vismia latifolia Aublet (V. ...
...
V. Aublet.
Negative # 8.5.242



Type Specimen

VISMIA LATIFOLIA (AUBL) CHOISY



VISMIA BILLBERGIANA BEURL.

latex of *V. baccifera* subsp. *ferruginea* is said to color fabrics with a fast color called "carate colorado" (*teste* F. R. Fosberg).

VERNACULAR NAMES

Some of the more frequent vernacular names applied to species of *Vismia* though without significant constancy for any one species include the following:

achiotillo (Venezuela, Colombia, etc.)	lacre (Amazonian drainage)
bloodwood (British Guiana)	pichirina (northern Peru)
caopia (Brazil)	punta de lanza (Colombia)
caparosa (Orinoco drainage)	sangrito (Venezuela), Colombia
capianga (State of Bahia, Brazil)	swinani (Carib name)
carate (Colombia)	

Additional vernacular names will be found in the text below and in S. J. Record and R. W. Hess's "Timbers of the New World," p. 186. 1943.

GENERAL MORPHOLOGY AND DESCRIPTIVE TERMINOLOGY

LEAF: The leaf-blades of *Vismia* species vary from thick, shining but concolorous structures on short stout petioles to thin-textured, deltoid, long-petiolate blades with a strongly bifacial aspect. The blades are mostly plane but may at times be plicate. Drip-tips are well developed in forms of *Vismia cayennensis*. The secondary veins may be weak to strongly impressed, camptodrome or simply diminishing towards the margin. Dot-like glands may be borne singly and centrally within an areole of fine veins, two or more may occur within an areole, or they may be absent altogether. There is no correlation between glandular-punctate leaves and vittate sepals or petals occurring together within a given group of species. When a leaf-blade is glabrous both above and beneath it is described as amphiglabrous, a term introduced in my studies of *Delphinium* (Univ. Colorado Stud. ser. D. 2:78. 1945) and employed in my revision of *Macrocarpaea* and elsewhere. The comparative anatomy of the leaves of *Vismia* species should prove an engaging study.

FLOWER: The inflorescence of *Vismia* is generally paniculate, but the panicle may be supplemented by lateral few-flowered axes borne in the upper leaf-axils. In *Vismia cauliflora*, the flowers are borne directly on the stems on short stalks. The sepals often have a scarious flange-like margin. The petals are generally comose within and glabrous on the back; there may be dark glands on one or both surfaces of the petals, called vittae, in which case the members are described as vittate. The androecium provides the fundamental basis for distinguishing subgeneric groupings. The stamens are connate for about half their length into what I have called a stamen

column ("staminal bundle" of Eyma,¹⁴ "androphora" of Bentham,¹⁵ or "phalange" of Reichardt¹⁶). The stamen column may persist as an almost wire-like stiff structure in old flowers, but usually shrivels after anthesis. The ovoid or globose anthers are included and dehisce longitudinally. The ovary does not offer significant differences usable in taxonomy. The five styles are generally coherent but may at times spread like antennae.

FRUIT: *Vismia baccifera* attracted the attention of the early systematists by its heavy, fleshy, smooth-coated fruits, which led to the recognition of the genus as distinct from the capsular-fruited *Hypericums*. But most *Vismias* have rather inconspicuous spherical to oblong berries with shriveled walls, these sometimes vittate with wart-like epidermal appendages but usually unmarked.

Systematic Treatment

Genus *Vismia*

Hypericum pro parte, sensu Jacq. (1760), L. (1764), L.f. (1781), Lamarck (1797).

Caopia Adans. Fam. 2:448. 1763.

Caspia Scop. Intr. 276. 1777.

Vismia Vandelli, Fl. Lus. Bras. Spec. 51, t. 3, fig. 24. 1788, *nomen conservandum*.

Acrossanthes Presl, Bot. Bemerk., in Abhandl. Boehm. Gesell. Wiss. V, 3:452. 1845.

Trees or shrubs, often with orange sap; leaves opposite, the blades oblong or narrowly ovate to deltoid-ovate, acute to truncate or cuspidate, short- to long-petiolate, exstipulate, glabrous or stellulate-tomentose, sometimes ferruginously so, punctate-glandular or without glands, sometimes lustrous on both surfaces; inflorescences terminal, simply paniculate or corymbose-paniculate or with supplementary lateral floriferous branchlets, or at times altogether lateral; sepals generally ovate, more or less prominently scarious margined; petals equaling or exceeding the sepals, often oblanceolate and densely comose within with matted hairs, the petal-blades lineate, vittate, or eglandular, glabrous on the back; stamens numerous, included, more or less united half their length into 3 or 5 staminal columns, the stamens tardily deciduous or persistent into fruiting stage, the anthers globose or ovoid; ovary 5-celled, each locule with numerous, seldom few ovules; styles 5, more or less free, at times prominently spreading in age; stigmas capitate or subcapitate; fruit a berry, the pericarp thick and fleshy or thin and withering, dark brown or blackish, some-

¹⁴ Eyma in Pulle, Fl. Surinam 3:66. 1934.

¹⁵ Hooker, London Journ. Bot. 2: 371. 1843.

¹⁶ Mart. Fl. Bras. 12¹: 195. 1878.

times vittate with black scab-like glands, the calyx usually persistent on the fruits.

TYPE (i.e. Standard Species): *Vismia cayennensis* (Jacq.) Pers.

Key to the Species

Flowers borne in sessile glomerules along the stems; leaf-blades pandurate-obovate, large, 35–65 cm. long **1. V. cauliflora**

Flowers paniculate; leaf-blades seldom as much as 35 cm. long.

Stamen column villous or comose, persisting as a stiff spreading appendage after flowering; leaf-blades shallowly cordate at base (or merely rounded in *V. lateriflora* and at times in *V. angusta*), the veins prominently raised beneath **SUBKEY A**

Stamen column not villous, or if hairy then soon deciduous after flowering; leaf-blades not cordate at base, the veins not very strongly raised beneath.

Flowers small, inconspicuous, usually very numerous (50–150 in an inflorescence or more, or only 5–8 in *V. billbergiana*); sepals less than 5 mm. long, often less than half as long as the petals; inflorescence shorter than the uppermost subtending leaves and hidden by them; leaf-blades finely black-glandular-dotted beneath (except in *V. rufa*) **SUBKEY B**

Flowers larger, generally fewer (mostly 40–80 in an inflorescence, or more numerous in *V. tomentosa* and *V. lehmannii*); sepals 5 mm. long or more, at least half as long as the petals; inflorescence generally exceeding the uppermost leaves or not hidden by them; leaf-blades with or without glandular dots on the lower surface.

Leaf-blades glabrous or glabrate on both surfaces (the immature blades sometimes puberulent in *V. lauriformis*); sepals 5–6 mm. long, spreading or reflexed in fruit (cf. also *V. amazonica* and *V. pentagyna*).

SUBKEY C

Leaf-blades variously pubescent beneath, varying from felty-tomentose to merely cinereous with a fine close puberulence under a lens (cf. also *V. rusbyi*); sepals 7–10 mm. long, more or less erect in fruit (5 mm. long in *V. amazonica* and *V. pentagyna*) **SUBKEY D**

SUBKEY A

Rachises of the panicle only sparsely tomentulose with scattered flocs of stellate hairs or subglabrous; leaves subglabrous or sparsely dark-tomentulose beneath, the tomentum not obscuring the fine sessile black dot-like glands, the blades usually lustrous above **2. V. macrophylla**

Rachises of the panicle densely rufous-tomentose throughout; leaves more or less copiously rufous-tomentulose beneath, the tomentum obscuring the glands (if these are present), the upper surface dull.

Rachises and upper stems heavily rufo-pubescent with long, much-branched hairs; leaf-blades both apiculate at apex and acute at base, long-petiolate.

3. V. sandwithii

Rachises pubescent but the hairs simple, rarely much-branched; leaf-blades either apiculate at apex or acute at base but not both, rarely long-petiolate.

Panicles terminal, ample, openly branching; leaf-blades cordate at base, thick, the principal nerves prominently raised beneath; petals comose, the hairs matted, wholly obscuring the blade of the petal . **4. V. angusta**

Panicles axillary (sometimes both axillary and terminal, rarely terminal alone), congested, compactly branching; leaf-blades truncate or subcordate at base, rather thin-textured, the principal nerves conspicuous but not raised beneath; petals ciliate-comose, the hairs not usually obscuring the blade of the petal **5. *V. lateriflora***

SUBKEY B

Panicle cymose, few-flowered (5-8); leaf-blade apiculate, the cusp 1 cm. long. **30. *V. billbergiana***

Panicle racemose, generally more than 8-flowered or if fewer then not cymose; leaf-blade acute but not strictly apiculate.

Under-surface of the leaves rich ferruginous-tomentose; sepals about 4 mm. long, felty-tomentose; stamen column very short, only 1.0-1.5 mm. long; leaves felty-tomentose beneath, not finely black-glandular . . **6. *V. rufa***

Under-surface of the leaves variously puberulent but never ferruginous-tomentose; sepals mostly 1.5-2.0 (3.0) mm. long, not felty-rufous-tomentose; stamen column more than 2 mm. long; leaves finely black-glandular beneath.

Each stamen column bearing 3 or 5 stamens; leaf-blade ovate, lance-ovate, or broadly ovate, hairy along the veins beneath; sepals without glands. Stamen column triandrous; leaf-blades acute at base, hairy chiefly along the veins beneath; fruit globose, coal-black, small (less than 5 mm. in diameter) **7. *V. micrantha***

Stamen column pentandrous; leaf-blades rounded or subcordate at base, puberulent over the whole blade beneath with short, crisp, white hairs; fruits ovoid, dull black, larger (more than 5 mm. in diameter).

8. *V. brasiliensis*

Each stamen column bearing numerous stamens; leaves lanceolate to oblong-lanceolate, not hairy along the veins beneath; sepals bearing glands. Sepals 3- to 5-nerved, punctate with a few scattered black, dot-like glands; petioles 10-12 mm. long **9. *V. parviflora***

Sepals with a single median raised confluent black gland; petioles 2-4 mm. long **10. *V. minutiflora***

SUBKEY C

Principal leaf-blades mostly (3) 7-12 cm. wide; petals 8-14 mm. long, mostly twice as long as the sepals or more (except in glabrous forms of *V. lauriformis*).

Sepals perfectly glabrous even in bud (rarely hairy at the tips); leaf-blades 3-7 cm. wide, ovate, less often lanceolate, acute at base, shining beneath.

43. *V. sprucei*

Sepals finely pubescent on the back; leaves 7-12 cm. wide, dull beneath.

Leaf-blades lance-ovate, acute at base; flowers not at all showy, the petals 5-7 mm. long; glabrous form of **25. *V. lauriformis***

Leaf-blades broadly ovate or ovate-oblong, rounded at base; flowers sometimes rather showy, the petals 7-9 (14) mm. long.

Leaf-blades ovate-oblong, often punctate, thin-textured, commonly wrinkling in drying, the veins prominently areolate, the secondary veins 6-10 pairs.

Petals 11-16 mm. long, very finely lineate for their whole length, sparsely vittate toward the tips; sepals 8-9 mm. long, the hyaline margin nearly obsolete; panicles always terminal . . . **23. *V. cuatrecasasii***

Petals smaller, 7–10 mm. long, black-glandular toward the tips but not finely lineate; sepals 4–5 mm. long, the hyaline margin distinct; panicles either terminal or lateral **42. *V. obtusa***

Leaf-blades broadly ovate, not punctate, firm-textured; veins anastomosing at the margin, inconspicuously if at all areolate, with usually 12 pairs of secondary veins or more.

Leaf-blades usually less than 15 cm. long, acuminate at apex, brownish, golden or silvery beneath, more or less contrasting with the green upper surface; petals glanduliferous **24. *V. baccifera***

Leaf-blades usually 15–20 cm. long, abruptly acute at apex, sooty or ashy beneath, hardly contrasting with the dark olive-green upper surface; petals not glanduliferous, usually merely vittate or dark lineate **41. *V. confertiflora***

Principal leaf-blades mostly less than 5 cm. wide; petals less than 8 mm. long, about half again as long as the sepals.

Sepals rusty or ashy with a close felt-like tomentum on the back (cf. also *V. glabra* with often thinly floccose-hairy buds); leaf-blades lanceolate, gradually acuminate, pinnately veined or areolate; petioles 1–2 cm. long.

Leaf-blades areolate-veined, thin-textured, dull on the upper surface, ovate. **36. *V. glaziovii***

Leaf-blades pinnately veined, firm-textured (usually not folding or wrinkling in drying), shining or dull above, generally lanceolate, often narrowly so.

Leaf-blades acute or acuminate, dull or less often shining and dark green on the upper surface; panicle not compact-pyramidal; widespread species **27. *V. guianensis***

Leaf-blades often shortly cuspidate, lustrous upper surface; panicle compact-pyramidal; eastern Brazil **35. *V. reichardtiana***

Sepals glabrous on the back (sometimes tomentulose in *V. plicatifolia*); leaf-blades ovate or lanceolate, the veins usually prominently areolate; petals always vittate-glandular outside; petioles 1 cm. long or less (1.0–1.5 cm. long in *V. glabra* subsp. *pozuzoensis* and *V. laevis*).

Leaf-blades lanceolate to oval, long-acuminate or merely acute but not apiculate, plane; fruit ovoid to fusiform, tapering to often persistent styles.

Leaf-blades 5–7 cm. wide, acute, coriaceous, the midrib stout; branchlets stout, stiffly spreading, the knoblike joints of pedicels prominent.

18. *V. laevis*

Leaf-blades 3.5–4 cm. wide, long-acuminate, firm but hardly coriaceous, the midrib not prominent; branchlets slender, the pedicels inconspicuously jointed.

Leaves spreading, the blades lanceolate, shortly acute or rounded at base; petioles 6–10 mm. long **19. *V. glabra* subsp. *glabra***

Leaves ascending, the blades oval, cuneate at base; petioles 10–15 mm. long **19a. *V. glabra* subsp. *pozuzoensis***

Leaf-blades ovate, shortly acute or apiculate, plane or plicate; fruit oblong to subglobose.

Tree 3–10 (35) m. high; internodes not noticeably short; leaves only moderately if at all plicate, generally markedly glandular-punctate beneath, the 1 to few black dot-like glands prominent within each areole **17. *V. cayennensis***

Shrub or low tree 2–3 m. high; internodes short; leaves strongly plicate, usually finely glandular-punctate beneath, the glands rather faint in the areoles **20. *V. plicatifolia***

SUBKEY D

- Calyx gibbously enlarged below, constricted above, the sepals all erect, the alternate sepals prominently hyaline-margined; petals included, short, 5–7 mm. long, tardily expanding **15. *V. urceolata***
- Calyx not urceolate; petals distinctly longer than the sepals, expanding early.
- Sepals broadly deltoid, 6–8 mm. wide at base, thick, proportionately narrowly hyaline-margined, hard or corky-ribbed in fruit; flowers few, mostly 5–12 in a rather compact short-pedunculate panicle **12. *V. japurensis***
- Sepals oblong or ovate, not deltoid; panicle more than 15-flowered or if fewer-flowered then not compact.
- Membranous border of sepals conspicuous, wide, ciliolate; sepals 5 mm. long. **40. *V. amazonica***
- Membranous border of sepals inconspicuous or if evident then not ciliolate; sepals 7–10 mm. long.
- Panicle freely and shortly branching, diffuse, with supplementary short lateral upper clusters, ample, 100–140-flowered.
- Sepals felty-tomentose, the tomentum dense dark chocolate-brown; flowers 10–12 mm. long; leaf-blades 18–24 cm. long, 10–13 cm. wide, the lower surface rich red-brown, finely hairy (under a lens) with discrete rufous hairs **29. *V. tomentosa*** forms
- Sepals pale- or yellow-green-pubescent; flowers 8–9 mm. long; leaf-blades 9–15 cm. long, 5–7 cm. wide, the lower surface silvery or yellowish, cinereous-puberulent beneath **22. *V. lehmannii***
- Panicle not both freely and compactly branching or if so then less ample, fewer than 100-flowered, the flowers generally 10 mm. long or more. Uppermost floral leaves reduced (except in *V. tomentosa* and *V. mandurr*).
- Outer surface of sepals permanently felty with a thick tomentum (cf. also *V. lateriflora*); petioles of even the uppermost leaves noticeably long (1–2 cm. long); sepals of fruiting calyx reflexed (spreading in *V. panamensis*).
- Leaves permanently felty-tomentose, thick-textured; sepals tomentose with a thick raised dark chocolate-brown tomentum.
- Leaf-blades narrowly lanceolate or oval, acuminate, 3–5 cm. wide, waxy-shining above, the veins obscure beneath . **32. *V. crassa***
- Leaf-blades ovate to broadly ovate, shortly acute, 6–11 cm. wide, dull above, the veins prominent beneath, areolate. **29. *V. tomentosa***
- Leaves more or less densely tomentose beneath when young, thinly tomentose in age, thinner in texture and wrinkling; sepals tomentose with an appressed brown or gray tomentum.
- Leaf-blades gray-tomentulose beneath, oval to elliptic, acute at base; pubescence of rachises and pedicels straw-colored; panicle cymose, compactly branching, with 3 axes or more. **26. *V. mandurr***
- Leaf-blades reddish-tomentulose beneath, ovate to oblong-ovate, rounded at base or if acute not also cinereous; pubescence of rachises and pedicels rufous; panicle more or less pyramidal with one principal axis.
- Flowers large, the petals nearly twice as long as the sepals, 14 mm. long, 5–6 mm. wide; leaf-blades 15–18 cm. long, glossy above; endemic species of central Colombia. **28. *V. cavanillesiana***

Flowers much smaller, the petals little exceeding or at most 1.5 times as long as the sepals; leaf-blades 7–12 cm. long or if 15–18 cm. long or more then not glossy above.

Leaf-blades 12–22 cm. long, 6–10 cm. wide; petals hardly exceeding the sepals; lowland forest of Pacific coast of Panama and northern South America.

14. *V. panamensis*

Leaf-blades smaller, 7–12 cm. long, 5–8 (10) cm. wide; petals 1.5 times as long as the sepals; species of eastern Brazil.

Leaf-blades broadly ovate, shortly acute; margins of calyx-lobes vittate with black glands; panicle subtended by many small supplementary leaves . . . **33. *V. martiana***

Leaf-blades oval to narrowly ovate, acuminate; margin of calyx-lobes without glands; panicle subtended by few if any small supplementary leaves . **34. *V. magnoliifolia***

Outer surface of sepals glabrous to variously puberulent but never with a thick felt-like tomentum, the veins or wrinkles clearly visible beneath the pubescence (cf. also *V. mandurr*); petioles mostly less than 1 cm. long (longer in *V. baccifera*); sepals of fruiting calyx spreading or appressed against the fruit (except in *V. baccifera*).

Mature leaf-blades 3–6 (8) cm. wide.

Leaves densely rufous-tomentose beneath with stellate or branched hairs at least when young.

Leaf-blades broadly ovate, shortly acute; margins of calyx-lobes black-glandular-vittate; panicle foliose . . . **33. *V. martiana***

Leaf-blades narrowly ovate, acuminate; margins of calyx-lobes without glands; panicle without supplementary leaves.

34. *V. magnoliifolia*

Leaves all merely cinereous or yellowish with a close puberulence beneath, sometimes appearing glaucous (reddish tomentulose in forms of *V. lauriformis*).

Branches of the panicle glabrous, puberulent, or with occasional flocs of short-branched hairs; leaf-blades ovate, elliptic- or lance-acuminate, the petioles slender.

Principal leaf-blades ovate to ovate-elliptic, rather abruptly acuminate, sometimes plicate, not at all falcate; sepals of the fruiting calyx strongly reflexed.

Petals not vittate; leaves strongly bicolored, dull above, conspicuously glandular-punctulate beneath.

37. *V. rusbyi*

Petals vittate; leaves not strongly bicolored, shining above, not punctulate (or obscurely so on the youngest blades), appearing more or less glaucous beneath.

38. *V. pentagyna*

Principal leaf-blades lance-acuminate, more or less long-tapering to a slender tip, not at all plicate; sepals of the fruiting calyx spreading.

Leaf-blades more or less falcate, dull above, glandular-punctulate beneath; petals black-glandular-vittate.

16. *V. falcata*

Leaf-blades ovate or narrowly lanceolate, not at all falcate, lustrous above, not punctulate beneath; petals not glandular-vittate.

Panicle many-flowered, compact-pyramidal; veins closed-areolate, distinct; petals densely villous-tomentose within **35. *V. reichardtiana***

Panicle few- and loosely-flowered; veins not areolate or weakly so; petals only thinly tomentose within.

39. *V. buchtienii*

Branches of the panicle ferruginous-tomentose throughout with branched hairs; leaves elliptic or lanceolate, not falcate, the petioles generally short, rather stout.

Leaf-blades oval or elliptic, 8–12 cm. long, 5–8 cm. wide, acute or abruptly acuminate, rather prominently areolate; fruit usually oblong, the sepals spreading to strongly reflexed.

Leaf-blades tapering equally at both ends or only shortly acuminate, strictly elliptic, 5–6 cm. wide; petioles 1–1.5 cm. long; sepals in fruit strongly reflexed.

31. *V. lindeniana*

Leaf-blades rather rounded at base, acuminate at apex, 6–8 cm. wide; petioles less than 1 cm. long; sepals in fruit spreading or somewhat reflexed . . **11. *V. sessilifolia***

Leaf-blades lanceolate, 8–12 cm. long, 3.5–4.5 cm. wide, tapering to an acuminate apex, not prominently areolate; fruit globose, the sepals not strongly reflexed.

21. *V. viridiflora*

Mature leaf-blades mostly broader, 7–13 cm. wide.

Leaves finely but densely punctate with minute dots . . **13. *V. latifolia***

Leaves not punctate beneath.

Leaf-blades uniformly rufous-tomentose beneath with stellate or branched hairs at least when young . **34. *V. magnoliifolia***

Leaf-blades all merely cinereous or yellowish puberulent beneath (or thinly tomentulose in *V. baccifera*).

Flowers not at all showy, the petals 5–7 mm. long; leaf-blades lance-ovate, acute at base, yellowish or cinereous beneath with a very fine close puberulence . . **25. *V. lauriformis***

Flowers rather showy, the petals 9–10 mm. long (7 mm. in *V. baccifera* subsp. *subcuneata*); leaves mostly broadly ovate (narrowly ovate in *V. baccifera* subsp. *ferruginea*), subtruncate or rounded at base, ferruginous, cinereous or canescent beneath.

Leaf-blades uniformly acuminate, tomentulose beneath with fine but discrete stellate hairs (as seen under a lens); petals glanduliferous with irregular black dot-like or welt-like glands **24. *V. baccifera***

Leaf-blades abruptly acute at apex, cinereous-puberulent beneath with minute simple hairs; petals usually non-glandular, often evenly lineate with fine dark lines extending to the tips of the blades . **41. *V. confertiflora***

1. *Vismia cauliflora* A. C. Smith, Journ. Arn. Arb. 20: 299. 1939.

TYPE: Along the road to Aleixo, Munic. Manáus, basin of Rio Negro, Amazonas, Brazil, *Krukoff* 7947 (NY; isotypes, A, BM, G, K, MO, S, U). Paratype from Livramento, Munic. Humaytá, basin of Rio Madeira, Amazonas, Brazil, *Krukoff* 6976 (A; dupl. paratypes, BM, G, K, S, U, US).

ADDITIONAL SPECIMENS EXAMINED:

BRAZIL: AMAZONAS: Colonia João Alfredo, Manaus, *Ducke* 930 (US); Estrada do Aleixo, *Ducke* 25055 (K).

Shrub-like tree 4–8 m. high, often with few, short branches. In some particulars this *Vismia* is the most distinctive species in the genus, though evidently rarely collected. Its affinities are clearly with *V. angusta*, but, as *Ducke* has commented,¹⁷ the sessile glomerate inflorescence alone would easily separate it from all other species. The striking leaves with blades measuring up to 65 cm. long, or longer than originally described, display an unusual shape recalling those of *Ficus lyrata* (*F. pandurata*); they are evenly narrowed for their lower half and shallowly cordate at the very narrow base. The common name is reported as “lacre.”

2. *Vismia macrophylla* H. B. K. Nov. Gen. & Sp. 5: 184. 1822. PLATE 2
Caopia macrophylla Kuntze, Rev. Gen. Pl. 1: 59. 1891.

V. macrophylla var. *glabrescens* Hochr. Ann. Cons. Jard. Genève 21: 53. 1919.

Type from “Prope San Gabriel de Cochoeira, ad Rio Negro, Brasiliae borealis,” *Spruce*, Jan.–Aug. 1852 (isotypes, BM, E, F, FI, Boissier at G, NY, P, TCD, W).

TYPE: Banks of Río Cassiquiare, Amazonas, Venezuela, *Humboldt & Bonpland* (P; isotype B, numbered 1151, Photo FM 9497); cf. *Sandwith*, Kew Bull. 1931: 174.

ADDITIONAL SPECIMENS EXAMINED:

SURINAM: Tawa Creek, Saramacca River headwaters, *Maguire* 23766 (NY, U, US); Groningen, 10 May 1916, *Samuels* (US).

BRITISH GUIANA: Aruka River, Barima, *Anderson* 40 (NY); Waini River, Northwest District, *de la Cruz* 3841 (NY, UC, US); Kamakusa, Upper Mazaruni River, *de la Cruz* 2115 (UC, US), 2383 (US), *Jenman* 5324 (BM, NY); Rockstone, *Gleason* 480 (US), 551 (US); Potaro River, Tumatumari, *Gleason* 340 (US); Essequibo River Basin, *A. C. Smith* 2162 (U, US); Barima River, *de la Cruz* 3382 p.p. (US); Upper Rupununi River, *de la Cruz* 1446 p.p. (US), 1744 (US); Malali, Demarara River, *de la Cruz* 2614 (UC, US); sand reef at head of Hoorubia Creek, southeast of Georgetown, *Hitchcock* 16950 (S, US); Demerara River, *Jenman* 5035 (BM); Good Hope, *Persaud* 44 p.p. (F); Berbice, *Schomburgk* 405 p.p. (CGE, F, FI, OXF, W); Kabakaburi, Pomeroon District, *de la Cruz* 3255 (NY, UC, US).

VENEZUELA: ZULIA: Río Lora, *Pittier* 10961 (US). TÁCHIRA: San Félix, *Curran & Haman* 1011 (US). BOLÍVAR: Río Karuai, west of La Laja, 1220 m., “minchu-warei-yek,” *Steyermark* 60784 (F, US); wooded slopes of Quebrada O-paru-má, between Santa Teresita de Kavanayén and Río Pacairao, 1065–1220 m., *Steyermark* 60434 (US); Roraima, *Schomburgk* 560 (P), 815 (BM, W). AMAZONAS: San Carlos, 100 m., *Holt & Gehrig* 331 (US).

COLOMBIA: BOLÍVAR: Palotal, *Romero C.* 1158 (US). SANTANDER: Quebrada Angulo, 4 km. south of Lebrija, 955 m., *St. John* 20589 (NO, US). META: Near junction of Río Güejar and Río Zanza, Cordillera Macarena, 500 m., *Smith & Idrobo* 1464 (US); 20 km. southeast of Villavicencio, *Killip* 34245 (US); Cano Ciervo, Sierra Macarena, 600 m., *Philipson et al.* 2088 (US). VAUPÉS: Mitú, Río

¹⁷ *Archiv. Serv. Florest.* 1: 34. pl. 13, figs. a, b. 1939.

Vaupés, *Cuatrecasas & Pérez-Arbeláez* 6750 (NY). CAQUETÁ: Solano, near Tres Esquinas, *Little* 9783 (NO, US). AMAZONAS: Leticia, *Schultes & Black* 46-317 (US). CHOCÓ: Darien region, *Dawe* 871 (K); Palestina, Río San Juan, 5-50 m., *Cuatrecasas* 16903 (US).

BRAZIL: AMAZONAS: Ega, *Poeppig* 2905 (F, W); along Rio Castanho, tributary of Rio Padauri, Upper Rio Negro Basin, 100-140 m., *Cardona* 1418 (US); São Paulo do Olivença, "lacre," *Ducke* 392 (A, F, US); San Gabriel de Cachoeira, *Spruce* (F, NY); Cachoeira Caranguejo, Rio Canabury, *Holt & Blake* 537 (US). MATO GROSSO: Rio Jatuarana, Rio Machado region, *Krukoff* 1692 (A, S).

Vismia macrophylla was widely misunderstood up to Sandwith's commentary on the species (Kew Bull. 1931: 174), in which he pointed out that Hochreutiner had misinterpreted the species and introduced a var. *glabrescens* "which agrees well with the type [of *V. macrophylla*]." The two sheets of the Spruce collection that served as the basis of var. *glabrescens* show the distinct black punctate glands of the lower leaf surface and the thinly tomentulose rachis of the panicle of *Vismia macrophylla*.

"Oralli" is the forester's name for *Vismia macrophylla* in British Guiana and one collection (Mazaruni Station, *Fanshawe* F627, US) is annotated "low branchy tree peculiar to swampy savannahs on white sand where it is co-dominant with *Tabebuia longipes*."

A West Indian collection of this species labeled in Walker Arnott's hand merely "St. Vincents (Dr. Hooker)" in the Glasgow Herbarium is almost certainly a cultivated specimen grown at the botanic garden on the island and communicated by Rev. Lansdowne Guilding to W. J. Hooker with whom he was in active correspondence.

The Triana collection "8," February 1856, from Llano San Martín, Villavicencio, Meta, Colombia, 400 m. (BM) cited by Triana and Planchon¹⁸ as *Vismia macrophylla*, represents the extreme form of this species. Triana's No. "7" from the same locality is very puzzling, combining as it does the flower characters of *V. macrophylla* with the leaf shape and vestiture of *V. baccifera* subsp. *dealbata*. On the other hand *Fendler* 8, from Chagres, at the mouth of the Chagres River, now in the Panama Canal Zone, represents a less frequent intermediate phase between this species and true *Vismia latifolia*. This Fendler collection is the basis of Sprague's doubt as to the correctness of Triana and Planchon's interpretation of *V. macrophylla*. But, judging from a photograph, *Fendler* 8 closely approaches the isotype collection (formerly at Berlin, but destroyed in World War II) in leaf shape, panicle characters, and the rather strong nervation. In many characters these collections stand between *Vismia angusta* and *V. macrophylla* and were it not for their fascicled stamens might be taken for a variant of *V. tomentosa*.

Two Brazilian collections, *Ducke* 1068 (NY, US), and *Corner* 63 (NY), from the vicinity of Manaus, Amazonas, are unique in the

¹⁸ Ann. Sci. Nat. IV. Bot. 17: 306. 1862.

abundance and character of the pepperlike black dot glands on the lower leaf-surfaces, which in these collections are so prominent as to show clearly through to the upper surface. The leaves furthermore are of an unusually thin texture for this species.

3. *Vismia sandwithii* Ewan sp. nov.

Arbor parva vel frutex 5 m. altus vel minus, ramis superioribus firmis subquadrangularibus, dense rufo-tomentosis, rache atque ramis conspicue subpannatis; laminis foliorum oblanceolatis vel obovatis, basi cuneatis vel vix cordatis, apice apiculatis vel caudatis, subtus atropunctatis, tomentosis, venulis supra subglabris, nitentibus, 18–30 cm. longis, 7–10 cm. latis; petiolis crassis, 1–2 cm. longis, rufo-tomentosis; paniculis compactis atque breviter ramosis; sepalis oblongis breviter acutis, 5–6 mm. longis, viridi-rufidulis dense tomentosis, intus viridescentibus, atro-vittatis; petalis oblongo-spathulatis, breviter acutis, ochroleucis, atro-vittatis, intus dense comosis; staminibus ad anthesin conspicuis filamentis persistentibus; fructibus immaturis conico-ovoideis, 1 cm. longis.

Small tree or shrub to 5 m. high, the upper branches stout somewhat quadrangular, densely, almost velvety rufous-tomentose with long, branched hairs; upper leaves little if at all reduced below the panicle and surpassing it, all the blades strongly bifacial, dark green, subglabrous and shining above, light green below, sparsely rufous-tomentose but densely so along the veins, the blades oblanceolate or obovate, apiculate at tip or even caudate, acute at base or at most weakly cordate, 18–30 cm. long, 7–10 cm. wide, the submarginal veins well-defined; petioles stout, 1–2 cm. long; panicle compact, shortly branching, 6–9 cm. long, the rachis and branches densely rufous-tomentose; sepals oblong, shortly acute, 5–6 mm. long, densely rufous-tomentose becoming greenish in fruit, greenish within, black-vittate; petals oblong-spatulate, acute, pale cream, densely comose on face, black vittate on back; stamen column conspicuous at anthesis, becoming indurated in fruit; immature fruit conic-ovoid, 1 cm. long, “pale green, brown-dotted.”

Type in the Royal Botanic Garden Herbarium, Kew, collected at Mahdia River, Potaro River, 107 miles on the Bartica-Potaro road, British Guiana, 8 January 1943, by an unrecorded collector for the Forest Department of British Guiana (no. 3726); isotype in the New York Botanical Garden.

PARATYPES:

BRITISH GUIANA: Mahdia River, Potaro River, Jan. 21, 1943 (fruit), *Forest Dept. B.G.* 3805 (K, NY); 111 miles Potaro River Road, May 10, 1952, *Forest Dept. B.G.* 6480 (K,U).

Vismia sandwithii is clearly an extreme morphological development of the *V. macrophylla-angusta* alliance. The bifacial leaves, their shape, venation, and apiculate tips are suggestive of *V. sessilifolia* and so this plant may prove to be a hybrid between that species

and *V. macrophylla*. Then too, the large floral leaves subtending the compact and at times lateral panicles suggest *V. lateriflora*. Although *V. macrophylla* and *V. angusta* represent "exceedingly variable populations" (cf. Maguire, Bull. Torrey Club 75: 417, 418. 1948), I am not including *V. sandwithii* within them because of its possible hybrid origin involving genetic relationships with *V. sessilifolia* as well as with *V. macrophylla*, and because of the extreme nature of its sepal, leaf, and pubescence differences. *Vismia sandwithii* is a small local population of coastal British Guiana where it has been described as a "very common" small understory tree or shrub in second-growth forest. One collection, (*Forest Dept. B.G.* 6480) mentions its growing on "ironstone gravel," another (3805), on "white sand," and the type collection (3726), "of all [types of] soils."

It is appropriate to associate this British Guiana *Vismia* with Noel Yvri Sandwith, of the Royal Botanic Gardens, Kew, who has botanized in British Guiana and who published on this genus in 1931, and who in many ways has assisted me in the present revision.

4. *Vismia angusta* Miq. *Linnaea* 18: 27. 1844.

?*Hypericum reticulatum* Poir. in Lam. *Encycl. Suppl.* 3: 694. 1813. Type from Cayenne, no collector designated, in Desfontaine Herb. at Paris. Sagot reports the Poiret type as consisting of a single leaf with no record of the country of origin. Sagot's drawing and short memorandum of the lost type, examined at Paris, are not sufficient to affect the rejection of Poiret's name as a *nomen dubium*.

?*V. reticulata* Choisy, *Prodr. Monog. Hyper.* 34. 1821.

V. macrophylla sensu Benth. in Hook. *London Journ. Bot.* 2: 371. 1843, as, for example, *Schomburgk* 405 (K); non H.B.K.

V. latifolia sensu Reich., in Mart. *Fl. Bras.* 12¹: 208. *t.* 38. 1878, excluding var.; non *V. latifolia* (Aubl.) Choisy.

?*V. latifolia* var. *reticulata* Reich. in Mart. *Fl. Bras.* 12¹: 208, 1878, as to basionym.

Caopia cordata Rusby, *Bull. N. Y. Bot. Gard.* 8: 105. 1912. Type: Apolo, Bolivia, 1440 m., *R. S. Williams* 99 (NY; isotypes, BM, K, US).

V. cordata Blake, *Contr. Gray Herb.* 53: 41. 1918.

TYPE: "Surinami ad Osembo in Para, m[ense] Aprilis 1842," *Focke* 382 (U). Eyma cited "584" in error.

ADDITIONAL SPECIMENS EXAMINED:

FRENCH GUIANA: Cayenne, *Martin* (BM); Godebert, *Wachenheim* 107 (K, US).

SURINAM: Without locality, *Hostmann & Kappler* 162 (MO, NY, P, S, U); Cottica River, *Lanjouw* 398 (U); Watramiri, *B.W.* 4543 (NY); Sectie O, *B.W.* 2711 (US), 2919 (NY); Zanderij I, *B.W.* 4362 (NY).

BRITISH GUIANA: Morabelli Creek, *Sandwith* 395 (K, NY, U); Mora Landing, Moruka River, *de la Cruz* 1853 (UC, US); Mazaruni Station, *Forest Dept. B.G.* 6469 (tree in open creek swamp 4 in. diam., 40 ft. high) (K); below Kaieteur, Potaro River, *Jenman* 977 (K).

VENEZUELA: BOLÍVAR: Río Karún, Alto Río Paragua, "uadama-yek," Cardona 1229 (US); Mojasilla, south of La Paragua, 75 m., "sangrito," L. Williams 12773 (US); Río Uairén, Sabanas de Santa Elena, Tamayo 2958 (US).

COLOMBIA: META: Between Villavicencio and Río Ocoa, 450 m., Dugand & Jaramillo 2917 (US); Villavicencio, Apiai, 500 m., Cuatrecasas 4772 (US); Villavicencio, Schiefer (US). PUTUMAYO: Quebrada del Río Mulato, Mocoa, Cuatrecasas 11305 (US). CAQUETÁ: Solano, near Tres Esquinas, 200 m., "lacre," Little & Little 9502 (NO, US). AMAZONAS-VAUPÉS: Soratama, Río Apaporis, Schultes & Cabrera 12724 (NO, US). TOLIMA: Falán, region of "Calamonte," 1120 m., "puntelanza," Garcia-Barriga 8377 (US). ANTIOQUIA: San Carlos, Kalbreyer 1374 (C); near Yolombó, Lehmann 4003¹⁹ (BM, K, US); [Río] Samaná, 500–1300 m., Lehmann 7547 (US); Mulatos, 50 m., Haught 4885 (NO, US). ?CAUCA: El Chorro, 800 m., March 1853, Triana (COL), same loc. no. "5" (BM). EL VALLE: Quebrada de La Brea, Río Calima, region of Chocó, 20–40 m., Cuatrecasas 21279 (US). CHOCÓ: Río Atrato, vicinity of Quibdó, 400 m., Araque-Molina & Barkley 19Ch 134 (NO, US, a variable coll.)

PERU: LORETO: Iquitos, ca. 100 m., Sandeman 2273 (K), L. Williams 1385 (F), 1460 (F), 1533 (F), Tessmann 3614 (NY), 5040 (G), Killip & Smith 26923 (US), 27221 (US); Mishuyacu, near Iquitos, "pichirina blanca," 100 m., Klug 888 (US); Pebas, Río Amazonas, L. Williams 1734 (US), 1748 (US); Maquisapa, Upper Río Nanay, L. Williams 1205 (F); Caballo-Cocha, Río Amazonas, L. Williams 2194 (US); Gamitanacocha, Río Mazán, 100–125 m., Schunke 133 (F, NA, NY, UC, US).

BRAZIL: Without locality, Sellow 159 (P.) AMAZONAS: Rio Embira, at Rio Tarauaca, basin of Rio Jurua, Krukoff (G, K, S, UC, US); San Jose de Rio Negro, Riedel 1427 (US). BAHIA: Without locality, Salzmann (P); Ilheos, Riedel 187 (US), Blanchet 1933 (C, F, FI, G, K, NY, W).

This widely distributed *Vismia*, a tree 4 to 12 meters high or more, is characteristic of selva borders or in Amazonian Brazil it grows on higher ground back from the seasonally inundated lands. Vernacular names, arising in most instances from the orange sap that bleeds freely from the cut stems, include: "Bloodwood" (British Guiana); "sangrito" (Amazonian Venezuela, Amazonas); "puntelanza" (Colombia); "lacre" (Amazonas). See Eyma²⁰ for Surinam vernacular names.

N. Y. Sandwith drew attention (Kew Bull. 1931: 174) to the identity of *Vismia angusta* as distinguished from *V. macrophylla* H. B. K., and determined the oldest name for this species, which long passed as *Vismia ferruginea*, to be Miquel's *V. angusta*. Eyma followed Sandwith in this conclusion.

The cordate leaf-base is a characteristic feature of *Vismia angusta* yet some Peruvian collections have a rounded leaf-base. Furthermore, these non-cordate specimens average to have distinctly smaller leaves. In British Guiana *V. macrophylla* likewise has cordate-based leaves.

¹⁹ A wrong number. In the Lehmann fieldbook (US), no. 4003 is listed as *Masdevallia*, an orchid.

²⁰ Pulle, Fl. Surinam 3: 75. 1934.

On Gorgona Island, off the Pacific Coast of Colombia (*Collenette* 588, K, US), *Vismia angusta* likewise exhibits smaller leaves which are not prominently cordate as is so characteristic of the species over its principal continental range. Perhaps this tree of Gorgona Island and the Peruvian-Colombian transmontane forests merits description as a subspecies of *V. angusta*.

Vismia angusta reaches its southern limit in Bolivia, where, as in the interior of Peru and Colombia, the leaves average smaller as noted above. Rusby's *Caopia cordata* was a collection of Bolivian *V. angusta* named for the cordate leaf-bases, which are conspicuous in the type collection.

Though the name *Vismia angusta* has been adopted for this distinctive species there is considerable evidence that the oldest valid name may prove to be *V. reticulata* (Poir.) Choisy. The basionym, *Hypericum reticulatum* Poir., rests on a good description and the source of the material, though not documented, might well have been from typical *angusta* territory. Neither Sandwith nor Eyma succeeded in locating the type. In view of the complex nature of this group of *Vismias* and the undoubted basis for the adoption of the name *V. angusta*, it has seemed in the interest of stability to regard *Hypericum reticulatum* as a *nomen dubium*.

TABLE 1.—*Comparison of the characters of Vismia angusta, macrophylla, and sandwithii*

<i>Vismia macrophylla</i>	<i>Vismia angusta</i>	<i>Vismia sandwithii</i>
<i>Tree</i> 2–5 (or 10) m. high at flowering time.	<i>Tree</i> 5–10 m. high or more at flowering time.	<i>Shrub</i> or <i>small tree</i> less than 5 m. high (?), the stem 5 cm. diam.
<i>Leaves</i> often thin-textured, ovate to ovate-lanceolate, acuminate, weakly cordate.	<i>Leaves</i> generally leathery, oblong, shortly acute, distinctly cordate at the base (except Gorgona Island and interior Colombia and Peru-Bolivia).	<i>Leaves</i> rather thin-textured, oblanceolate or obovate, cuneate, apiculate to caudate, acute or at most weakly cordate.
<i>Secondary veins</i> prominent or at times rather faint, esp. toward tip of blade.	<i>Secondary veins</i> generally all very prominent, raised below.	<i>Secondary veins</i> rather faint toward tip of blade.
<i>Submarginal veins</i> indistinct.	<i>Submarginal veins</i> indistinct.	<i>Submarginal veins</i> prominent, well defined.
<i>Petioles</i> 1.5 cm. long or more.	<i>Petioles</i> usually 1 cm. long or less.	<i>Petioles</i> 1–2 cm. long.
<i>Rachis of inflorescence</i> glabrate in age, with only flocs of persistent brown tomentum of stellate hairs.	<i>Rachis of inflorescence</i> permanently rusty-tomentose with stellate hairs or tardily deciduous- to floccose-tomentose.	<i>Rachis of inflorescence</i> conspicuously densely rufous-tomentose, branching hairs almost velvety.

TABLE 1.—*Comparison of the characters of Vismia angusta, macrophylla, and sandwithii—Continued*

<i>Vismia macrophylla</i>	<i>Vismia angusta</i>	<i>Vismia sandwithii</i>
<i>Flower buds</i> dark fuscous to almost blackish.	<i>Flower buds</i> light yellowish brown.	<i>Flower buds</i> rufous.
<i>Flowers</i> without odor (?).	<i>Flowers</i> fragrant.	<i>Flowers</i> without odor (?).
<i>Petals</i> obovate, greenish, tomentose on inner face but not so densely as to obscure the blades.	<i>Petals</i> linear-spatulate, whitish or cream-colored, so heavily comose as to obscure the blade, the hairs often twice as long as the width of the petal.	<i>Petals</i> oblong-spatulate, acute, whitish, densely comose on face, black-guttate on back.
<i>Fruit</i> globose, green.	<i>Fruit</i> globose to ovoid, green or olive-brown.	<i>Fruit</i> conic-ovoid, pale green.
<i>Sepals</i> 4–5 mm. long; veins usually obscured by dense tomentum.	<i>Sepals</i> 4–5 mm. long; veins evident beneath tomentum.	<i>Sepals</i> 5–6 mm. long, the tomentum so dense as to obscure the venation.

5. *Vismia lateriflora* Ducke, Arquiv. Serv. Florest. Rio Janeiro 1: 33. 1939.

LECTOTYPE: Esperança, at the mouth of Rio Javary, Amazonas, Brazil, Ducke 25054 (isolectotype, K). Syntype: Presidente Marquez Station, on the Madeira-Mamoré Railway, Mato Grosso, Brazil, Kuhlmann 21223 (duplicate syntypes, K, US).

ADDITIONAL SPECIMENS EXAMINED:

COLOMBIA: Río Loretoyacu, Trapecio amazónico, 100 m., Schultes & Black 8448 (US), 8449 (US).

PERU: [probably Huánuco but without loc.] Dombey (F). Cuzco: Cerro San Pedro, 1600 m., Vargas 8504 (US). LORETO: Pebas, L. Williams 1793 (F); La Victoria, Río Amazonas, L. Williams 2691 (F); Caballo Cocha, L. Williams 2192 (F), 2364 (F); Soledad, Río Itaya, 110 m., Killip & Smith 29689 (F, US); Maynas, Poeppig 421 (P); Mishuyacu, Iquitos, 100 m., "pichirina," Klug 354 (F, US); Iquitos, 100 m., Killip & Smith 27085 (F, US); Yurimaguas, Lower Río Huallaga, 155–210 m., L. Williams 3821 (F), 4899 (F, US), 5003 (F, US), Killip & Smith 27550 (US); San Antonio, Río Itaya, 110 m., Killip & Smith 29475 (F, US). HUÁNUCO: Pampayacu, 1050 m., Macbride 5019 (F).

BRAZIL: AMAZONAS: Near Tres Casas, basin of Rio Madeira, Munic. Humaytá, Krukoff 6325 (A, G, S, U, US, W); near Palmares, basin of Rio Solimões, Munic. São Paulo de Olivença, Krukoff 8328 (A, G, K, P, S, U, US).

Vismia lateriflora may prove to be but a seasonal phase of *V. angusta* with axillary inflorescences produced through suppression of the usual terminal panicle, induced perhaps at times of exceptional water supply or by some other microclimatic factor. Still, the oblong leaves of *V. angusta* are dull above, whereas the ovate, acute leaves of *V. lateriflora* are more or less shining above as if varnished. *Vismia angusta* typically has distinctly cordate leaves, the midrib and secondaries prominently raised beneath, and marginal or submarginal areolate venation. Its spherical flower buds, opening tardily, are

yellowish-green or sulphur-colored on the outside, the petals heavily yellowish comose, with the hairs often so long as to extend beyond the petals, forming a kind of tuft in the center of the flower. *V. lateriflora*, on the other hand, has ovate leaves of a distinctly thinner texture, a truncate or at most subcordate base, and the nerves not prominently raised beneath, areolate with loop veins well inside the leaf margin. Moreover, the flower buds in *Vismia lateriflora* are long-ovoid, early opening, brownish on the outside, the petals less densely comose, the hairs not exceeding the petals. The pubescence of the lower leaf surfaces of the two species is similar but in *V. angusta* it has a dusky quality, due to the presence of minute black glands, one gland to each areole of the lower leaf surface. In *V. lateriflora* the thin-tomentulose lower leaf surface is distinctly reddish and, though the minute dark glands are present in this species as well, they are obscure. Though the lateral axillary panicles especially characterize *V. lateriflora*, both lateral and terminal inflorescences may occur (e.g., *Macbride* 5019 and *Krukoff* 8328), or, again, lateral panicles may be wholly absent and only the terminal ones present. In this connection, *V. ramuliflora*, which might from the name be thought to be an earlier name for this species, is, in fact, a synonym of *V. sessilifolia*, of the coast of northern South America.

6. *Vismia rufa* Cuatrecasas, Rev. Acad. Colomb. Cienc. 7: 47. fig. 1. 1946.

TYPE: Forest, Río Cajambre, Department of El Valle, Colombia, 5–80 m., 5–15 May 1944, *José Cuatrecasas* 17449 (Comision de Bot. del Valle, Cali, Colombia) (isotypes, NY, US).

ADDITIONAL SPECIMENS EXAMINED:

COLOMBIA: EL VALLE: La Trojita, Río Calima (region of Chocó), 5–50 m., *Cuatrecasas* 16614 (US); hills near Quebrada de la Brea, Río Calima (region of Chocó), 30–50 m., *Cuatrecasas* 21102 (US); near Buenaventura, April 8, 1882, *J. Ball* (K).

Vismia rufa is a tree 16 to 30 meters tall, the trunk 25 to 40 centimeters in diameter, the bark dark reddish-brown, scaly and breaking into narrow rough plates from longitudinal cracks; wood soft-textured, red; latex bleeding bright orange-red; leaves thick, leathery, conspicuously petiolate, the petioles 12–25 mm. long, subterete or grooved on the upper side, the blades ovate or ovate-elliptic, shortly acute, 11–18 cm. long, 4.5–7 cm. wide, lustrous-shining and glabrous above, the midrib impressed, strikingly rufous beneath with a heavy felt-like tomentum; inflorescence much-branched, sometimes few-flowered and lateral but generally with very numerous small crowded flowers in a diffuse panicle; sepals early spreading, ovate-oblong, small, 3.5–4.5 mm. long, narrowly hyaline-margined, evenly ferruginous-tomentose on the back; petals a little longer than the sepals, thick-textured, spatulate-ovate, rounded at the tips, roseate, vittate with a few dark

lines; stamens reddish, very short, about half as long as the ovary; fruit unknown.

This interesting endemic *Vismia* of the Pacific rain forests of Colombia is most singular for its small flowers, a character not evidently appreciated by Cuatrecasas as significant when the tree was described. Its taxonomic position may be near *V. brasiliensis*, judging from the five small stamen-columns, the rufous-tomentose leaves, and the ample panicle of numerous crowded flowers, but the leaves are wholly unlike that Brazilian species, recalling rather *V. cavanillesiana*.

7. *Vismia micrantha* Mart. ex St. Hilaire, Fl. Bras. Merid. 1: 327. 1827; Mart. in Spix & Mart., Reise Bras. 2: 552. 1828.

Trianthera floribunda Pohl ex Reich. in Mart. Fl. Bras. 12¹: 198. 1878, pro syn. *V. micranthae*. Authentic material from Villa Rica, Brazil, E. Pohl 3738 (F, W).

Caopia micrantha Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: Syntypes "in sylvis et campis provinciae Minas Geraës prope San Gabriel, vicum vulgo Catas Altas, urbem Villa Rica, et in monte Serra Negra," presumably referring to St. Hilaire collections, now at Paris. Presumably authentic material for the Spix & Martius description: Without locality, *Martius* 970 (BM, G, K, L, MO, P, W, WU).

ADDITIONAL SPECIMENS EXAMINED:

BRAZIL: MINAS GERAIS: Serra de Ouro Preto, en route to Antonio Pereira, *Schenck* 3577 (C); Ouro Preto, *Riedel* 2634 (K); Morro de Cruzeiro, Ouro Preto, *Damazio* 1328 (G); Serro de Cipó, Munic. Santa Luzia, *Barreto* 1274 (F); "Minas sylvis montosis," *Riedel* 25 (P); Monte Itacoluni, Santa Luzia, *Casaretto* 3510 (G); Monte Capanema, *Riedel* 1474 (S); São Juliaõ, Santa Luzia, *Schwacke & Glaziou* (P); Ressaca, Bello Horizonte, *Barreto* 2910 (F); Serra do Caraça, Munic. Santa Barbara, *Barreto* 2912 (F).

Tree; leaves rather thin, more or less green on both surfaces, the blades short-ovate, 6–10 cm. long, 3–4 cm. wide, finely glandular-punctate and often thinly hirtellous beneath, especially along the veins, with mostly simple hairs; panicle often very compound, rather compact, the flowers numerous; sepals oblong, rounded, thinnish, with no or a barely distinct marginal flange, glabrate; petals about twice as long as the sepals, cream-colored, obovate, tomentulose within, punctate on the back with black glands; stamen column bearing 3 anthers; ripe fruit globose to short-pyriform, black, 4 mm. long, usually tipped with 5 persistent styles, the sepals spreading.

Vismia micrantha is easily distinguished from all other species by the unique character of its stamens, but a certain affinity with *V. brasiliensis* is suggested by characters of both the foliage and the inflorescence. It will be noted that both species differ from the section *Euvismia* in having a reduced number of stamens borne on a single stamen column. These two *Vismias* are in fact not easily distinguished in sterile condition. However, the secondary veins in *Vismia micrantha* in anastomosing at or near the margin unite by a weak con-

necting vein, this often freely branching. In *V. brasiliensis*, on the other hand, the secondaries anastomose by a single strong connecting vein, without branches to the margin. The shape, size, and pubescence of the leaves of the two species are very similar, but on the whole *V. micrantha* has thinner leaf-blades than those of *V. brasiliensis*. The tomentulose sepals of *V. brasiliensis* often contrast easily with the glabrate sepals of *V. micrantha*; the fruit of the former is larger and generally the styles are earlier deciduous than those of *V. micrantha*.

8. *Vismia brasiliensis* Choisy, Prodr. Monog. Hyper. 35. t. 2 1821.

V. longifolia St. Hil. Fl. Bras. Merid. 1: 326. t. 68. 1827. TYPE: "In sylvis caeduis prope tabernam vulgo Rancho de José Henriquez, haud longe ab urbe Villa Rica, in provincia Minas Geraës; florebat Januario," Brazil, St. Hilaire. Not distinguished among the St. Hilaire colls. at Paris. The illustration though generalized in details is conclusive evidence of its taxonomic position here.

V. laccifera Mart. in Spix & Mart. Reise Bras. 2: 552. 1828. TYPE: A Martius collection, presumably from the vicinity of Villa Rica, in the state of Minas Gerais, Brazil. St. Hilaire evidently saw the manuscript description of Martius' species prior to its publication the following year, for he refers to it in 1827 (in his Fl. Bras. Merid. 1: 326. 1827). Reichardt evidently believed *laccifera* to be a typographical error for *baccifera*, and ignored it as a synonym of *brasiliensis*; however, *laccifera* was supported by a full description, which shows it to be a synonym of *brasiliensis*.

V. brasiliensis var. *lasiantha* Reich. in Mart. Fl. Bras. 12¹: 198. 1878. TYPE: Sellow 530, from Brazil (Delessert Herb. and Boissier Herb. G, GL, K, L, W, fragments of isotype ex Geneva, F; Photo FM 9166, of specimen in Berlin Herbarium).

V. lasiantha Klotzsch ex Reich. in Mart. Fl. Bras. 12¹: 198. 1878, *pro syn.*

V. brasiliensis var. *longifolia* Reich. in Mart. Fl. Bras. 12¹: 198. 1878.

Caopia brasiliensis Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: "In Brasilia", according to the description but not so labeled, simply "Mr. Steven, 1820" (in de Candolle Herb., G). The name ticket is in the hand of Choisy. The plate, drawn directly from the specimen, is too generalized in detail, and fails to show the thin pubescence on the lower leaf-surfaces, the lineate-guttate sepals, and the fine hairs of the pedicels.

ADDITIONAL SPECIMENS EXAMINED:

BRAZIL: SÃO PAULO: Penha, in 1839, *Guillemin* 498 (G), Jan. 1840, *Guillemin* 498 (TCD); Jardim Botânico, São Paulo, *Hoehne* 198 (F, S; this no. at A and G is *V. micrantha*). MINAS GERAIS: Jardim Botânico, Bello Horizonte, *Barreto* 2909 (F); Serra do Taquaril, *Barreto* 2908 (F); Matta de Empreza, *Barreto* 4035 (F); Lagoa Santa, *Warming* (C); Caa do Campo, *Claussen* 3 (F), *Claussen* 4 (FI, G, W); Caldas, *Regnell* III 298 (FI, S, US, WU); Gongo-soco, Jan. 1825, *Riedel* (NY, US); "on border of the forest Gongo-Soco," in 1834, *Bunbury* (CGE); without locality, *Claussen* 134 (BM, K).

Tree; leaves rather thin, generally green on both surfaces, the blades ovate or short-ovate, 6–10 cm. long, 3–7 cm. wide, finely glandular-punctate and generally simply hirtellous beneath, especially pubescent along the veins with both simple and branched hairs; panicle rather

compactly branching, the flowers numerous, the whole inflorescence cano-tomentulose; sepals oblong-ovate, bordered by a distinct flange-like membranous margin, tomentose over the back with a close felt-like tomentum; petals about 1.5 times as long as the sepals, obovate, cream-colored, densely tomentulose within, punctate with black glands on the back; stamen column bearing 5 anthers; ripe fruit pyriform or globose, acute, dull black, 4–9 mm. long, the styles persistent.

Vismia brasiliensis comprises two distinguishable geographic races, a more northern and southern Brazilian race, and each has been named in the past and maintained as varieties by Reichardt. The Minas Gerais race, which tends toward longer leaves and only moderately tomentose flowers, is evidently St. Hilaire's *V. longifolia*. The São Paulo race, with short-ovate leaves, recalling those of the garden apricot in size and texture, and with truly lanuginous flowers, is what Klotzsch designated in the herbarium as *V. lasiantha*. Choisy's type evidently represents this southern phase, but if so the pubescence is somewhat deciduous from the fruiting branchlets. Both forms are inconstant and many more collections from the vast regions of Brazil are needed before a clear conclusion may be reached.

Vismia brasiliensis has been compared with *V. micrantha* under the latter species. The leaves of *V. brasiliensis* generally have a slightly developed cordate base, and the blades tend to be plicate, a condition not seen in *V. micrantha*.

St. Hilaire listed three *Vismias* for central Brazil,²¹ namely, *V. longifolia*, *V. guianensis*, and *V. micrantha*. When he described *V. longifolia* he overlooked Choisy's recent publication of *V. brasiliensis* (1821) or its inclusion in the account of the genus in de Candolle (1824). *V. longifolia* was described by St. Hilaire as having "staminibus 25–30." It is singular that if he was describing a phase of *V. brasiliensis* he did not refer to the distinctive character of that species, namely, that each stamen column bears only five stamens. However, Reichardt aligned *V. longifolia* with *V. brasiliensis*, and certainly the very detailed original description of *V. longifolia* is not out of harmony with *V. brasiliensis*.

It is possible that the "Ubapitanga" of Marcgrav (Hist. Nat. Brasil. 293) and his "Caopia arbore ejusque facultatibus" (op. cit. 60), accompanied by a crude line drawing of a thick-leaved plant with variable-shaped leaves and globose fruits, may represent *Vismia brasiliensis*. If so, it constitutes the earliest mention of this *Vismia*, or, indeed, of any Brazilian *Vismia* in literature.

We may be much more certain of the fact that the *Vismia* described by Vandelli when he established the genus (1788) was *V. brasiliensis*,

²¹ Fl. Bras. Merid. 1:325–328. 1827.

for he characterized it as having "filamenta plura in 5 phalanges s[ive] corpora connata." *V. brasiliensis* was certainly therefore the original species of the genus, although it was not so chosen when *Vismia* was conserved. Vandelli indicates the origin of his *Vismia* by the initial "B," meaning Brasilia.

9. *Vismia parviflora* Schlecht. & Cham. Linnaea 3: 119. 1828. PLATE 3
Caopia parviflora Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: "Brasilia tropica," Sellow (B, Photo FM 9168, which carries a ticket reading "Sello 1365") (Isotype CGE).

"*V. Calycibus pellucidis 3-nervibus subpunctatis, petalis punctatis, phalangibus triandris calyce brevioribus, stylis longis, foliis ellipticis nigro-punctatis, pilis sparsis.*

"In Brasilia tropica collegit Sellow.

"Folia elliptica v. elliptico-lanceolata, acuminata, saepius in ovatum rarius in obovatam vergentia formam, basis subinde inaequali acuta vel rarius obtusa rotundata, acumine brevi subtrilineari saepe obliquo, submembranacea, quam in congeneribus paullo tenuiora, subtus punctulata, punctis opacis nigris prominentibus, obsitaeque pilis stellatis rufescentibus sparsis; maxima 4 poll. longa. 1½ lata, petiolo semipollicari. Rami novelli cum petiolis, panícula alabastrisque tomento tenui rufo-canesciente oblitterante obducti. Panícula multiflora, laxiflora, quam in congeneribus uberior, pyramidata, e ramorum primariorum paribus circiter sex constans, quam panícula Syringae persicae paulo minor.—Flores brevissime pedicellati, parvi, expansi 2 lin. circiter metientes. Lacinae calycinae ellipticae, obtusae, lineam circiter longae, subpellucidae, 3–5 nerves, evittatae, nunc punctis resinosis paucis (rarius 6), in aliis aliter dispositis, notatae, nunc omino impunctatae. Petala elliptica, obtusa, calyce longiora, intus villis brevibus parce obsita, punctis resinosis irregulariter adspersa. Staminum phalanges calyce breviores, omnino glabrae, triandrae, filamento medio longiori supra tertia parte libero. Squamae villosae, subspathulatae, phalangibus paulo breviores. Germen glabrum. Styli 5 longiusculi, filiformes, e calyce demum exserti, stigmate depresso-capitato. Fructus—?"

Vismia parviflora is a rare species evidently closely related to *V. micrantha* but that species has vittate sepals. Prior to my visit to the Paris Herbarium I had not seen any collection of this *Vismia* and rested my disposition of what is certainly a distinctive species on the original description, reproduced here, and the Macbride photograph of the type, Sellow's collection in the Berlin Herbarium having been destroyed. However, one collection of *Vismia parviflora* came to light in Paris: "Minas Gerais, 1816–1821," St. Hilaire D55 (P). Dwyer²² identifies this St. Hilaire collection as one taken in 1821–22 when he visited the provinces of Rio de Janeiro (nos. 1–30), Minas Gerais (31–587) and São Paulo (588–818). There is a second collection, Minas Gerais, 1841, Claussen 5 (P), which is referred to this species with reservations. It is notable that no recent collections of *Vismia parviflora*, evidently of extreme local occurrence in Brazil, have been made.

²² Ann. Missouri Bot. Gard. 42:162. 1955.

10. *Vismia minutiflora* Ewan, sp. nov.

Arbor parva vel frutex 2.5 m. altus, ramis superioribus gracilibus, fissuratis, griseo-brunneis, raches atque ramis rufo-tomentulosis, inferioribus glabrescentibus; foliis superioribus non reductis, laminis omnibus submembranaceis, ovato-lanceolatis, 7–9 (13) cm. longis, acuminatis vel cuspidatis, ad basim breviter acutis vel subrotundatis, amphiglabris, infra atro-punctatis, supra venis impressis; petiolis brevibus, 2–4 mm. longis; paniculis compactis et brevi-ramosis; sepalis minimis, 1.5–2 mm. longis, flavibus, partibus centralibus atro-pubescentibus; petalis breviter oblongis, albis, atro-vittatis, intus sparse comosis; staminibus ad anthesin exsertis; fructibus ignotis.

Small tree or shrub 2.5 m. high or more, the trunk slender, the branchlets clothed with thin gray-brown bark splitting into narrow shreds, rufous-tomentulose with fine branched hairs on young wood and rachis of the panicle, glabrescent below; leaves little if at all reduced at the inflorescence and exceeding it, thin, amphiglabrous except at the extreme base beneath where weakly stellate-pubescent, finely black gland-dotted beneath and impressed-venose above, ovate-lanceolate, 7–9 (or 13) cm. long, acuminate to cuspidate, shortly acute or barely rounded at the base, the petioles slender, short, 2–4 mm. long; flowers short-pedicellate, the panicle compactly and shortly branched; calyx very small, 1.5–2 mm. long, yellowish with a narrow central black pubescent ridge, spherical in bud; petals short-oblong, white, vittate with impressed black glands, rather lightly comose within; stamens exceeding the corolla at anthesis; fruit unknown.

Type in the U.S. National Herbarium, No. 1,795,145, collected at San José del Guaviare, Río Guaviare, Intendencia of Meta, Colombia, in savana, alt. 240 meters, Nov. 11, 1939, by José Cuatrecasas (No. 7658); isotypes in the herbaria of the Royal Botanic Garden, Kew, and the New York Botanical Garden.

PARATYPES:

PERU: Río Azara, Upper Río Marcapata, east of Urcos, 1050 m., *Sandeman* 3730 (K); Moro, 1200–1500 m., Jan. 1866, *Pearce* (K); “Perou,” *Gay* 939 (P).

The affinities of *Vismia minutiflora* are with the section *Vismia* and not with the section *Trianthera*, to which *Vismia micrantha* belongs, as might well be expected upon the basis of the small flowers, although the combination of characters shown in *Vismia minutiflora* are not closely approached by other species of the section *Vismia*. The leaves recall *Vismia cayennensis* but are thinner and more herbaceous. The short-pedunculate panicle suggests a species of *Sambucus*, an impression further borne out by the small flowers crowded into small cymules. Individually, the flowers are rather showy for their white petals which far exceed the exceptionally small calyx.

A Peruvian collection, *Klug* 2344 (A, US), from the mouth of the Río Zubineta, near Florida, Río Putumayo, Department of Loreto, has

much larger leaves, 12–14 cm. long, and a more compound diffuse panicle—quite unlike the Colombian type collection from the Río Guaviare. In points of flower structure this Peruvian collection is in agreement, but the curious callosities on the sepals and the unusual twisting of the long petals suggests a diseased plant. Aside from the short-petiolate leaves, *Klug* 2344 resembles the type collection of *Vismia parviflora* in several particulars.

11. *Vismia sessilifolia* (Aubl.) DC. Prodr. 1: 542. 1824. PLATES 4, 5

Hypericum sessilifolium Aubl. Pl. Guian. 2: 787. t. 312, fig. 2. 1775.

H. rufescens Lam. Encycl. 4: 150. 1796. TYPE: Aroura, a village opposite the Isle of Cayenne (cf. Bellin's map of 1763), French Guiana, 17–21 Nov., 1785, *Stoupy* (P, Photo FM 35239, Photo Killip 911).

V. rufescens Pers. Syn. Pl. 2: 86. 1806.

V. rufescens var. *sessilifolia* Pers. loc. cit.

V. ramuliflora Miq. Stirp. Surinam 88. 1850. TYPE: "Sylvis umbrosis regionum interiorum," Surinam River, Surinam, April 1847, *Hostmann & Kappler* 1823 (holotype, U; isotypes, G, S; Photo FM 35238, of specimen in Paris Herbarium).

Caopia sessilifolia Kuntze, Rev. Gen. Pl. 1: 59. 1891.

Caopia sessilifolia var. *rufescens* Kuntze, loc. cit.

TYPE: Cayenne, *Aublet* (holotype, BM, Photo NY; isotype, G–DC). *Gleason* 64 (US) is a close match for *Aublet*'s figure.

ADDITIONAL SPECIMENS EXAMINED:

FRENCH GUIANA: Maroni, *Wachenheim* 58 (E); Karouany, *Sagot* 65 (BM, S, W), 69 (P); Godebert, *Wachenheim* 49 (P); Roura, 1859, *Sagot* (P).

SURINAM: Patrick Savannah, *B. W.* 672 (NY, U); Sectie O, *Krukoff* 12315 (NY); Grote Zwiebelzwamp, *Lanjouw & Lindeman* 1255 (U).

BRITISH GUIANA: Vicinity of Kartabo Station, junction of Mazaruni and Cuyuni Rivers, *Graham* 292 (US); Arawak Matope, Cuyuni River, *Tutin* 374 (BM, U, US); Tumatumari, Potaro River, *Gleason* 64 (NY, US); Potaro, 10 miles south of Potaro Landing, *Hitchcock* 17389 (US); Waini River, *de la Cruz* 3730 (UC, US); Kurupung, Tacoba, *Lang & Persaud* 286 (F); Barima River, *Jenman* 7017 (NY); "Roraima," *Schomburgk* 917 (BM, CGE, FI, G), certainly from lowlands, possibly from Venezuelan side of boundary, where essentially all of *Schomburgk*'s collections originate.

VENEZUELA: Angostura, *Humboldt & Bonpland* 1070 (H. & B. Herb., P).

COLOMBIA: EL CHOCÓ: Istmina, *Killip* 35453 (US). CAUCA: Córdoba, Dagua Valley, 30–100 m., *Pittier* 511 (US). EL VALLE: Buenaventura, *Killip* 11734 (US); Road to Buenaventura, 400 m., *Triana* 6 (COL); Río Dagua, 10 km. from Buenaventura, *Core* 1519 (NO).

BRAZIL: PARÁ: Faro, Campos do Tigre, *Ducke* 12494 (K).

In *Vismia sessilifolia* the lower surface of the leaves has a close fulvous or rufous pubescence with usually a single, raised, dot-like gland in a single areole; the upper surface is not impressed-reticulate, as are both *V. baccifera* and *lauriformis*. The leaves in this species are oblong-ovate, shortly acuminate, the petioles short, noticeably broad, often wing-margined, the blades rather bifacial, glabrous and shining, green above, reddish-puberulent beneath with a thin deciduous scattering of fine hairs. The sepals are narrowly ovate, acute,

tomentulose on the back, about half as long as the narrowly oblong petals.

Though most often with petioles about 1 cm. long, *Vismia sessilifolia* occasionally has subsessile leaves, and it was this form that Aublet described and illustrated as *Hypericum sessilifolium*. Gleason describes his sessile-leaved collection (no. 64) as from a "shrub 15 feet high." The types of the two forms, the petiolate *rufescens* (Pl. 3) and the subsessile *sessilifolia* (Pl. 4), came from the same district of Cayenne and I cannot separate the two on any geographic grounds. Persoon aligned the sessile-leaved plant as a variety of *Vismia rufescens*, and de Candolle admitted both as full species and even placed them some distance apart in his treatment of the genus in the *Prodromus*, but it does not seem necessary to give them taxonomic recognition.

Vismia sessilifolia develops lateral axillary racemes either along with, or in the absence of, the usual terminal inflorescence, and it is this latter condition that led Miquel to distinguish *V. ramuliflora*. Miquel believed its relationship to be with *V. cayennensis*, overlooking *V. sessilifolia* and Persoon's *V. rufescens*. Nearly all the specimens cited that are in flower bear at least some reduced axillary racemes. I cannot determine any morphological basis for Miquel's proposed species. Incidentally, the Amazonian *V. lateriflora*, which might be presumed to belong here, is rather a relative of *Vismia angusta*.

Vismia sessilifolia is one of the most clearly marked species of the genus. However, Eyma did not admit it in his account of the flora of Surinam, an omission the more singular in that Eyma particularly concerned himself with the typification of species of Guttiferae of Surinam. Triana's collection from the vicinity of Buenaventura, 400 meters, agrees well with Choisy's plate²³ and with the photograph of Stoupy's type at Paris of *Hypericum rufescens* Lam. Neither Triana and Planchon, who remark on this Buenaventura collection, nor Sandwith mention having examined the Stoupy specimen at Paris.

12. *Vismia japurensis* Reich. in Mart. Fl. Bras. 12¹: 209. t. 39. 1878.

Caopia japurensis Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: "Prov. do Alto Amazonas in silva ad ripas fluminis Japura," Martius.

SPECIMENS EXAMINED:

SURINAM: Zanderij I, Maguire & Stahel 25053 (K, NY, US).

BRITISH GUIANA: Pomeroon River, Pomeroon District, *de la Cruz* 3149 (F, UC, US), 3170 (F, UC, US); Adaro River, Mazaruni drainage, near Wupaima Mountain, *Pinkus* 166 (NA, US); Bootooba, Demerara River, *Persaud* 16 (F); Canister Falls, Demerara River, *Beccari* 16 (FI, K); "Massaroonie & Cuyounie," *Appun* 277 (K).

²³ Prodr. Monog. Hyper. t. 1. 1821.

VENEZUELA: BOLÍVAR: Cerro Sarisarinama, Alto Caurá River, 800 m., *Cardona* 386 (US). AMAZONAS: Maroa, Río Guainía, 127 m., *L. Williams* 14348 (US); San Carlos, Río Negro, 100 m., *Holt & Gehriger* 297 (US), 302 (US), *L. Williams* 14478 (US), *Holt & Blake* 633 (US); Sabana de Río Sanariapo, 120 m., *L. Williams* 16003 (US), 13064 (US); Yavita, 128 m., *L. Williams* 13912 p.p. (US).

COLOMBIA: META: Puerto López, 240 m., "papa de lacre," *Little & Little* 8252 (NO, US). VAUPÉS: Vicinity of Raudal de Yuruparí, *Gutierrez & Schultes* 931 (MEDEL, US). CAQUETÁ: Sucre, 1000–1300 m., *Cuatrecasas* 9047 (US). AMAZONAS-VAUPÉS: Raudal Yayacopi, Río Apaporis, *Schultes & Cabrera* 15404 (NO, US).

BRAZIL: Without locality, *Burchell* 9697 (K, L), 10042 (K). AMAZONAS: Tapurucuará, Rio Negro, *Schultes & López* 8954 (US); São Gabriel, Rio Negro, *Holt & Blake* 599 (US); Yucabi, *Tate* 966 (NY); Manáus, Rio Negro, *Ule* 5964 (G, L). PARÁ: Belém, *Archer* 8053 (US), 8243 (US).

Vismia japurensis is at once recognizable for its deltoid, acute sepals which are noticeably thick, so that the fruiting calyx is almost woody. The ovate leaves appear nearly glabrous beneath, but are actually puberulent with microscopic golden glands. The leaf-base is nearly shallowly cordate at times, but, unlike *Vismia macrophylla* with which it might be confused, the peduncle and rachis of the panicle are merely puberulent, not at all conspicuously tomentose. The fruits are few, globose, and more pulpy than those of *Vismia macrophylla*.

13. *Vismia latifolia* (Aubl.) Choisy, Prodr. Monog. Hyper. 36. 1821. PLATE 6
Hypericum latifolium Aubl. Pl. Guian. 2: 787 and 4: t. 312, fig. 1. 1775.
Caopia latifolia Kuntze, Rev. Gen. Pl. 1:58. 1891.

TYPE: Cayenne (BM, photo, NY).

ADDITIONAL SPECIMENS EXAMINED:

SURINAM: Brownsberg, *B. W.* 1676 (L, US), 2372 (K, NY), 2869 (K, NY); Zanderij I, *B. W.* 459 (S), 1404 (K, NY), 1564 (K, L, NY); Paramaribo, *Splitgerber* 184 (L); Forest of Zandery, *Samuels* 275 p.p. (L, K).

FRENCH GUIANA: Rowea, Mar. 1859, *Sagot* (K); Cayenne, *Martin* 27 (BM); Maroni, in 1864, *Melinon* (NY).

Small tree about seven meters high. Apparently a well-known forest tree in Surinam, judging from the number of vernacular names mentioned by Eyma in Pulle's *Flora of Surinam*, but few collections seem to have reached herbaria.

Sandwith drew attention (Kew Bull. 1931: 174) to the long persisting confusion of this *Vismia* with *V. angusta*. The few collections seen, however, do not uniformly conform to Aublet's description of the leaves as "superne viridibus, inferne tomentosis, rufescentibus." The inflorescence is congested and the flowers are small but in the collections seen the sepals and fruits are blistered with a plant disease which may have affected their development. A noteworthy character not stressed in the literature is the narrowly oblong, abruptly acutish sepals, which form an oblong-ellipsoid flower bud very truncate at the base.

14. *Vismia panamensis* Duchass. & Walp. Linnaea 23: 748. 1850.

Caopia panamensis Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: "Panama," *Duchassaing*, probably from the vicinity of Panama City.

SPECIMENS EXAMINED:

CANAL ZONE: Ancón Hill, *Gillespie* P-12 (DS); woods at Gatún, *Hayes* 921 (NY).

COLOMBIA: EL CHOCÓ: Small quebrada opposite Palestina, Río San Juan, 0-5 m., *Cuatrecasas* 21389 (US). EL VALLE: Río Cajambre, 5-80 m., *Cuatrecasas* 17120 (US), 17551 (US); Puerto Merizalde, Río Naya, 5-20 m., *Cuatrecasas* 14081 (US); La Trojita, Río Calima, 5-50 m., *Cuatrecasas* 16354 (US); La Cuarantena, Buenaventura Bay, *Killip & Cuatrecasas* 38976 (US); Quebrada de Aguadulce, Bahía de Buenaventura, 0-10 m., *Cuatrecasas* 19738 (US); between Isla de Golondro and La Amargura, Río Yurumanguí, 10-40 m., *Cuatrecasas* 16068 (NO, US).

ECUADOR: ESMERALDAS: Mangrove swamp, San Lorenzo, near Río Nadadero, "sangre de gallina," *Marrero & Little* 6274 (NY, US).

Vismia panamensis is here interpreted as a lowland rain-forest tree of the Pacific Coast from Panama to Ecuador, having much the aspect of *V. lauriformis* on the one hand and of *V. baccifera* subsp. *ferruginea* on the other, and is probably most closely related to the former. The leaves of *V. panamensis* are more prominently venose than those of *V. lauriformis*, and these together with the leaf axils, rachises, etc., are much more rufous-tomentellous. *V. panamensis* is altogether a more heavily pubescent plant than *V. lauriformis*, from the stellate-tomentulose pedicels to the rich rufous-tomentulose sepals that remain erect in flower. *V. panamensis* is distinguished from *V. baccifera* subsp. *ferruginea* by the more heavily tomentose leaves which remain tomentose when the plant is in flower, and by the petals being only a little longer than the sepals, these twice as long in *V. baccifera* subsp. *ferruginea*.

Triana and Planchon examined a *Duchassaing* collection at Montpellier, the type of *Vismia panamensis*, and referred a Triana collection from Susumuco, Colombia, to that species. I have not seen a specimen or photograph of a *Duchassaing* collection, but I have studied a Triana sheet from Susumuco (now in Meta, near the Cundinamarca boundary) preserved at Bogotá (COL), which probably is a duplicate of the collection referred to by Triana and Planchon. Susumuco is out of the expected range of *V. panamensis*, but the Triana collection is a close match for a Panama specimen made by N. J. Andersson, April 1852 (US). I am suggesting that Triana's "Susumuco" collection of *V. panamensis* was taken, not in the interior of Colombia but in the Chocó, where we know he botanized,²⁴ and that a mixture of labels ensued.

²⁴ Cf. A. Dugand, Rev. Acad. Colomb. Cienc. 5: 488. 1944.

15. *Vismia urceolata* Ewan, sp. nov.

Arbor parva 5 m. alta, ramis gracilibus, apicibus puberulentis, deorsum glabris; laminis foliorum ovatis vel lanceolato-ovatis, acuminatis, 10–11 cm. longis, 4–5 cm. latis, non crassis, supra obscuris, infra minute cinereis vel brunneo-puberulentis praecipue secus nervos tenuiter (vel non) glandulosis, omnibus petiolatis, petiolis saepe reflexis, prominentibus, ca. 2 cm. longis; paniculis parvis, paucifloris, 4–5 cm. longis; calycis valde urceolatis vel deorsum gibbosis, 7–8 mm. latis, apice abrupte acutis, 9–10 mm. longis, deorsum aliquantum glabris, lobis persistente clausis, tantum erectis ad anthesin, ferrugineo-tomentulosis, marginibus hyalinis latis, minute atosanguineo-vittato-glandulosis; petalis auguste ovatis fulvis, lineatis, intus comosis ad apicem; staminibus inclusis.

Small tree 5 m. high, with gray smooth bark, the branchlets puberulent above, glabrate below; leaf-blades ovate or lance-ovate, 10–11 cm. long, 4–5 cm. wide, rather thin-textured, dull above, finely cinereous or brownish puberulent beneath, especially along the nerves, only microscopically glandular-punctulate (if at all), the secondary veins faintly anastomosing to form a submarginal vein, the petioles slender, rather prominent, often reflexed, about 2 cm. long; flowers few, loosely clustered in small panicles 4–5 cm. long; calyces strongly urceolate, enlarged below, 7–8 mm. wide, abruptly tapering to an acute summit, 9–10 mm. long, glabrate below, the lobes tardily spreading, and merely erect at anthesis, ferruginous-tomentulose on the back, the broad hyaline margin prominent, very finely black vittate-glandular; petals only a little exceeding the calyx, narrowly ovate, dark brown, finely lineate, comose on the inner face near the tips; stamens included; fruit unknown.

Type in the U.S. National Herbarium, No. 2,166,544, collected in cutover flood-plain forest of Río Meta, Puerto López, Intendencia of Meta, Colombia, alt. 240 meters, July 28, 1944, by Elbert L. Little, Jr., and Ruby Rice Little (no. 8275); isotype in the herbarium of Tulane University.

Vismia urceolata, known only from the type collection, is perhaps restricted to the llanos of Colombia. The urceolate calyx distinguishes this *Vismia* at once from all other species. From the leaf characters, habit, and panicle characters it is evidently most closely related to *V. lauriformis* of cismontane Colombia.

The collectors record the vernacular name "lacre" for this species. I am grateful to Dr. Little for the opportunity to study this and his other *Vismia* collections.

16. *Vismia falcata* Rusby, Descr. S. Amer. Pl. 59. 1920.

V. angustifolia Rusby, Descr. S. Amer. Pl. 59. 1920. **TYPE:** Sacupana, Venezuela, April 1896, *Rusby & Squires* 141 (holotype, NY; isotypes, A, BM, E, G, K, MO, US, W, WU).

TYPE: Santa Catalina, Lower Orinoco River, Venezuela, May 1896, *Rusby & Squires* 142 (holotype, NY; isotypes, BM, K).

ADDITIONAL SPECIMENS EXAMINED:

TRINIDAD: Cumuto, *Broadway* 5726 (UC); Caroni, *Eggers* 1420 (US), *Britton & Mendelson* 837 (US); Arima, *Eggers* 1118 (E, UC, US); (?) Mount Tucouche, *Broadway* 5291 p.p. (A, UC, young shoots); (?) Blanchisseuse Road, *Broadway* 5661 (UC); "Fl. Trinitatis," *Sieber* 100 (E, G).

TOBAGO: Bacolet, *Broadway* 4139 (S, US, W); without locality, May 6, 1925, *R. O. Williams* (NY).

BRITISH GUIANA: Kamakusa, Upper Mazaruni River, *de la Cruz* 2819 p.p. (UC, US, somewhat atypical); Rockstone, *Gleason* 481 (US); Barima River, *Jenman* 7017 p.p. (NY); Demerara River, *Jenman* 5029 (NY); without locality, *Schomburgk* 182 (GL, US).

VENEZUELA: BOLÍVAR: Roraima, *Schomburgk* 935 p.p. (CGE); Guayapo, Bajo Caurá River, 100 m., "sangrito rastrojero," *L. Williams* 11754 p.p. (UC, US); La Paragua, 285 m., *Killip* 37579 (US).

BRAZIL: AMAZONAS: (?) San Carlos, Rio Negro, *Spruce* 3115 (MO, P).

Vismia falcata is marked by its usually falcate peach-like leaves, borne on slender petioles. The thin, crisp blades measure 3 to 4 times as long as broad, tapering to a slender acuminate tip. The leaves are finely puberulent, punctulate beneath with black pepper-dot glands.

Vismia falcata is certainly closely related to *V. lauriformis*. Some collections from the State of Bolívar, Venezuela, suggest morphological points of kinship with *V. lauriformis* in having broader ovate leaves and a more diffuse panicle than usual.

Two of the Trinidad collections, *Broadway* 5291 and 5661, suggest another and possibly unrecognized *Vismia*. These specimens show smaller leaves, long-acuminate at the tips, the surface more shining above and more suggestive of *V. guianensis*. It is noteworthy that *Broadway* 5291 comes from the summit of Mt. Tucouche, a locality recognized for its peculiar flora, as yet only partially known.

The Brazilian collection, *Spruce* 3115, is variable; a sheet in the Meisner Herbarium (NY) is very much like typical *V. falcata*, but another (NY) is broader leaved, like *V. guianensis*.

17. *Vismia cayennensis* (Jacq.) Pers. Syn. Pl. 2: 86. 1807.

Hypericum cayennense Jacq. Enum. Pl. Carib. 28. 1760.

H. acuminatum Lam. Encycl. 4: 150. 1796. TYPE: Herb. Lamarck from "Aroura, [a precinct of] Cayenne," French Guiana, *Stoupy* (P, Photo FM 35234, Photo Killip 712). Type labeled "ex roura in 17 au 21 novembre 1785."

Vismia acuminata Pers. Syn. Pl. 2: 86. 1806.

H. eugeniaefolium Willd. ex. Spreng. Syst. Veg. 3: 351. 1826, *pro syn.* Based on *Humboldt* coll. (no. 1038) from Curichana, Orinoco, Venezuela, in Willdenow Herb. (Photo FM 9498). Authentic specimen in *Humboldt & Bonpland* Herb. (P).

V. latifolia var. *acuminata* Sagot, Ann. Sci. Nat. VI, Bot. 11: 163. 1881.

Caopia acuminata Kuntze, Rev. Gen. Pl. 1: 59. 1891.

C. cayennensis Kuntze, op. cit. 58.

Vismia floribunda Sprague, Trans. Bot. Soc. (Edinburgh) 22: 428. 1905.

TYPE: Mocoa, Caquetá [now Com. Putumayo], Colombia, *Sprague* 401 (holotype, K; isotypes, BM, US).

TYPE: Not designated by Jacquin, but undoubtedly from Cayenne, French Guiana (cf. Jacq. Stirp. Amer. 213. 1763).

ADDITIONAL SPECIMENS EXAMINED:

TRINIDAD: Arima, *Eggers* 1363 (US); Toco Road, Valencia, *Britton, Hazen & Mendelson* 1778 (NY, US); Fort St. Georges Hill, *Johnston* 106 (US); Ortoire River, Guayaguayare Road, *Britton, Freeman & Nowell* 2542 (US); Caroni River, south of Dabadie, *Britton & Hazen* 724 (US); Caroni North Bank Road, *Britton & Mendelson* 824 (US).

TOBAGO: Big River Bridge, Mason Hall, *Broadway* 3035 (L, NY); Greenhill, *Broadway* 4140 (S, US); Cocoaawatee, 15 Jan. 1913, *Broadway* (US); Bacolet River, *Eggers* 5731 (S, US).

FRENCH GUIANA: Karouany, *Sagot* 66 (G, K, NY, S, W); Cayenne, 1792, *Leblond* (A, NY); Cayenne, 1838, *Leprieur* (K, NY); Godebert, *Wachenheim* 40 (K, US); vicinity of Cayenne, *Broadway* 399 (NY, US), 209 (NY).

SURINAM: Raleigh Falls, Coppename River, *Lanjouw* 972 (NY); Kabelstation, *Lanjouw* 1180 (NY); Tamarinal, Cottica River, *Linder* 105 (NY); Charlesburg, near Paramaribo, *Lanjouw* 96 (U); near Oude Ryweg, Paramaribo, *Samuels* 212 (A), 213 (S); Juden-Savanne, *Kappler* 1722 (G, S); Charlesburg Rift, 3 km. north of Paramaribo, *Maguire & Stahel* 22779 (NY, US); Tawa Creek, *Maguire* 23765 (NY, US); forest of the Station, Groningen, *Samuels* 112 (A, K); Scotelweg, "swinani," "pina," *Archer* 2660 (NA, S, US), 2706 (NA, US); without locality, *Hostmann* 438 (BM, CGE, DS, G, K, OXF, S); Sectie O, *Maguire & Stahel* 23624 (US), *B.W.* 635 (US), 1772 (US).

BRITISH GUIANA: Without locality, *Schomburgk* 607 (CGE, G, GL, K, S, US); Pirara, *Schomburgk* 240 (BM, FI); Mabaruma Compound, "bloodwood," *Archer* 2304 (K, US); Kamakusa, Upper Mazaruni River, *Lang* 370 (NY); Isherton, Basin of Rupununi River, *A.C. Smith* 2443 (K, S, US).

VENEZUELA: AMACURO: Manoa, *Rusby & Squires* 143 (US). ANZOÁTEGUI: Cabeceras de Guaraguara, *Pittier* 14843 (US); Río Cochama, Mesa de Guanipa, 240 m., *Pittier* 14331 (US). BOLÍVAR: Quebrada O-paru-má, between Santa Teresita de Kavanayén and Río Pacairao, 1065–1220 m., "minchu-wareiyek," *Steyermark* 60423 (US); Medio Caurá River, Salto de Pará, 170 m., *L. Williams* 11472 (US); Sabana de Guayapo, Bajo Caurá River, 100 mi., *L. Williams* 11863 (US); La Paragua, 70 m., *L. Williams* 12612 (US); between Ciudad Bolívar and Río Caroni, 100 m., *Steyermark* 57579 (US); Gran Sabana, between Kun and Ruémerú, south of Mount Roraima, 1065 m., *Steyermark* 59142 (US); vicinity of Tumeremo, 305 m., "sangrito," *Steyermark* 60936 (US); Ciudad Bolívar, *Holt & Gehriger* 190 (US), *Bailey & Bailey* 1335 (US). AMAZONAS: San Carlos de Río Negro, 100 m., "lacre blanco," *L. Williams* 14529 (US).

COLOMBIA: BOLÍVAR: San Martín de Loba, *Curran* 67 (US). VAUPÉS: San Felipe, below confluence of Río Guainía and Río Cassiquiare, Río Negro, ca. 180 m., "puinave," "teen-ká," *Schultes, Baker, & Cabrera* 18083 (US). CAQUETÁ: Morelia, 150 m., *von Sneider* 1318 (US). AMAZONAS: Leticia, Trapecio amazónico, 100 m., *Schultes* 8208 (US); Río Humacayacu, Trapecio amazónico, above 100 m., *Schultes* 8252 (US). EL VALLE: Prov. Buenaventura, 1200 m., July 1853, *Triana* 3 (BM, COL).

ECUADOR: SANTIAGO-ZAMORA: Above Valladolid, Río Valladolid, 2100–2400 m., *Steyermark* 54726 (US).

PERU: SAN MARTÍN: Zepelacio, near Moyobamba, 1200–1600 m., *Klug* 3455 (F, K, S, US). LORETO: Yurimaguas, Lower Río Huallaga, 135 m., *Killip & Smith* 27580 (US), 28205 (US); Iquitos, 100 m., *Killip & Smith* 27039 (F, US).

BRAZIL: AMAZONAS: Near Livramento, on Rio Livramento, Munic. Humaytá, *Krukoff* 6865 (A, US); Paranagua, basin of Rio Jurua, *Krukoff* 4566 (A, US); road to Boa Vista, Caracarahy, *Froes* 22948 (NY); Ega, *Poeppig* 2532 (W); Esperança, mouth of Rio Javari, *Ducke* 1882 (US); Cucuhy, Rio Negro, 120 m., *Holt & Gehriger* 373 (US); Amapa, *Huber* 1219 (G); Manáus, 25 m., *Killip & Smith* 30089 (US); near mouth of Rio Embira, tributary of Rio Tarauaca, *Krukoff* 8479 (S, US); Parintins, *Ducke* 117 (US); near Palmares, Munic. São Paulo de Olivença, *Krukoff* 8479 (S, US). PARÁ: Santarém, August 1850, *Spruce* (E, G, NY, TCD).

Vismia cayennensis and *V. glabra* are very close in nearly all morphological characters. The buds of *V. glabra* are hairy on the outside, and those of *V. cayennensis* glabrous. The most noticeable feature of *V. glabra* is that the panicle-branches are pubescent right up to the peg-like swelling upon which each pedicel articulates; sometimes this swelling is clothed with a minute fringe of hairs. *V. cayennensis* is without this pubescence. The leaves of *V. glabra* are often larger than those of its relative but this is not uniformly true.

When Persoon established *Vismia cayennensis* he did not mention the earliest use of the epithet by Jacquin, but by following back through the literature by way of Willdenow,²⁵ to whom Persoon refers, the ultimate name-bringing basionym is established.

In Humboldt, Bonpland, and Kunth's "Nova Genera et Species Plantarum," *V. acuminata* (Lam.) Pers. is included on the basis of a specimen collected near Curichana, on the Río Orinoco near the confluence of the Río Meta. I have examined the Humboldt and Bonpland collection at Paris and find that it represents almost typical *V. cayennensis*. It does not have the long-acuminate leaf-tips of the form described as *acuminata*. The sheet bears the *nomen nudum* *Hypericum eugeniaefolium* Willd., indicated as a synonym by Sprengel.

18. *Vismia laevis* Triana & Planch. Ann. Sci. Nat. IV. Bot. 17: 303. 1862.

Caopia laevis Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: "Forêts du Quindio, alt. 2000 metres, prov. de Mariquita et forêts d'Antioquia (Tr.)." The first syntype is represented by a specimen "Forêts du Quindio, 1400 m.," *Triana* 262 (K). The second syntype is represented by "Prov. Antioquia, 2000 [meters ?], n.v. 'carate,' Mayo 1852," *Triana* 1 (COL, Photo U.S. Nat. Herb. 2967). The latter is designated as lectotype; isolectotypes, BM, P, Photo FM 35235.

ADDITIONAL SPECIMENS EXAMINED:

COLOMBIA: ANTIOQUIA: Río Negro, Medellín, 2100 m., *Sandeman* 5552A (K), 5712 (K), *Archer* 313a (US); La Sierra, 2000 m., *Archer* 1323 (NY, US); Llano Grande, near Río Negro, 2200 m., "punta de lanza," *Daniel* 3852 (US); Santa Elena, 2500 m., *Ríos C. et al.* 619 (US); San Pedro, "carate," *Tomás* 168

²⁵ Sp. Pl. 3: 1439. 1803.

(US); La Ceja, *Daniel* 2197 (US); Alto Catatumbo, north of Yarumal, 2300 m., *Core* 620 (NO). CALDAS: Portachuela, Quindio, 1844, *Goudot* (P). TOLIMA: El Líbano to Murillo, in subpáramo, 2200–2900 m., *García-Barriga* 12261 (US).

Vismia laevis, a relative of *V. cayennensis*, is an endemic species of central Colombia, characterized by longer, more narrowly lanceolate leaves than those of its relative, the blades tapering to long-acuminate tips, the texture distinctly more coriaceous. The sepals are more prominently hyaline-bordered, with a distinct broad flange. The pedicels are stout, peg-like, and tend to persist on older fruiting branchlets. The fruits average larger than those of *V. cayennensis* (12–20 mm. long), and are fusiform rather than subspherical, with conspicuous spreading or reflexed sepals. In certain of these characters *V. laevis* stands between *V. cayennensis* and *V. glabra*.

19. *Vismia glabra* Ruiz & Pav. Syst. Veg. Peruv. Chil. 183. 1798.

Caopia glabra Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: "Peru," without further indication. An authentic specimen in the Delessert Herbarium (G, Photo FM 23954) received from Pavon is designated as lectotype; there is another specimen in the Delessert Herbarium (G, Photo FM 8005) which is presumably a duplicate. Other authentic collections, perhaps isotypes: ex Herb. Lambert (BM), ex Herb. Pavon (K), and Herb. Boissier (G). Possible isotypes are "*Dombey* 640" (P) and "Cochero, *Dombey*" (P). Another collection *Dombey* 639, without locality (F) may be a syntype.

ADDITIONAL SPECIMENS EXAMINED:

PERU: LORETO: Above Pongo de Manseriche, 205 m., "pichirina," *Mexía* 6306 (CAS, F, S, UC, US); Pumayacu, *Klug* 3140 (A); Mishuyacu, near Iquitos, 100 m., *Klug* 1009 (F, US); Paraiso, Alto Río Itaya, 145 m., *L. Williams* 3366 (F), *L. Williams* 41 (F), 136 (F), 3310 (US); San Antonio, Río Itaya, 110 m., *Killip & Smith* 29410 (US), *L. Williams* 3324 (F), 3396 (F); Iquitos, 100 m., *Killip & Smith* 27075 (F, US), *Tessmann* 3659 (G, NY); Pebas, Río Amazonas, *L. Williams* 1639 (F); Caballo-Cocha, *L. Williams* 2061 (F); Yurimaguas, Lower Río Huallaga, *Killip & Smith* 27987 (F, US); Lower Río Nanay, *L. Williams* 357 (F). SAN MARTÍN: Upper Río Huallaga, *L. Williams* 5826 (F); San Roque, 1350–1500 m., *L. Williams* 7043 (US), 7044 (US); Tarapoto, *Mathews* 1310 (CGE, GL), *L. Williams* 5546 (F). HUÁNUCO: La Purísima, Distrito Churubamba, 1750 m., *Mexía* 8232 (F, K, NA, S, U, UC, US); Pampayaco, *Poeppig* 1020 (G, W, with remarkable ferruginous raceme branches).

BRAZIL: AMAZONAS: São Paulo de Olivença, near Palmares, Rio Solimões Basin, *Krukoff* 8479 (A, US); Rio Macaúhan, basin of Rio Purus, Rio Acre, *Krukoff* 5241 (UC, US); Cobija, Rio Acre *Ule* 9613 (K, Photo FM 9171 of a specimen in the Berlin Herbarium), 9639 (K); Seringal, Taraguassu, *Ule* 9909 (K, Photo FM 9172 of a specimen in the Berlin Herbarium).

Vismia glabra is a polymorphic species, the distinguishable forms being more or less correlated with the topography of the central Andes and their adjacent plains. Some forms are so strongly marked as to their vegetative features as to have been named, although not published, by Melchior of the Berlin Herbarium. The Amazonas collections—and there are many in our herbaria—are marked by unusually thin leaves borne on slender petioles, at more or less right

angles to the stem and long-pedunculate, loosely-flowered panicles. However, the flowers do not differ in their technical characters from those of the usual *Vismia glabra* of higher elevations in the Andes. These Amazonas collections commonly display lateral as well as terminal panicles, recalling *V. lateriflora* from the same region in this particular.

Vismia glabra is certainly most closely related to *V. cayennensis*, and, indeed, some collections are not easily identified; the *differentiae* are discussed in the account of *V. cayennensis*.

Although there was no mention made of Dombey collections when the species was described, *Dombey* 639 (F), consisting of merely a small but mature leaf, agrees closely with the leaf characters of the authentic collections preserved at Geneva.

19a. *Vismia glabra* subsp. *pozuzoensis* (Engler) Ewan, comb. nov.

V. pozuzoensis Engler, Bot. Jahrb. Engler 58, Beibl. 130: 1. 1923.

TYPE: Pozuzo, Department of Huánuco, Peru, N. Esperto (Photo FM 9170, of a specimen in the Berlin Herbarium).

SPECIMENS EXAMINED:

PERU: CAJAMARCA: Tambillo, *Jelski* 252 (S, US, W). HUÁNUCO: Moyobamba, *Weberbauer* 4515 (G); Cueva Grande, near Pozuzo, *Macbride* 4763 (F); Pozuzo, *Macbride* 4574 (F). JUNÍN: Carpapata, *Soukup* 3434 (US). Without locality, *Mathews* 1310 (BM).

BOLIVIA: SANTA CRUZ: Yungas de San Mateo, 2500 m., *Steinbach* 8403 p.p. (S).

Resembling typical *Vismia glabra* but the leaves strongly ascending, the blades oval, cuneate at the base, rather thick or firm, plane, sometimes punctate beneath with pin-point pits, the petioles 10–15 mm. long; panicles loosely fewer-flowered, often lateral as well as terminal; flower buds often ferruginous-woolly on the outside.

This subspecies is evidently restricted in its range. It is described as a “compact shrub or small tree” of “sunny brushy slopes” by J. F. Macbride, who has collected it at the type locality. Plants that appear to represent the same subspecies, though geographically at some distance from the Peruvian stations, have been collected in the Trapecio amazónico, Department of Amazonas, Colombia: Río Loretoyacu, 100 m., *Schultes* 8264 (US), 6691 (US), *Schultes & Black* 8389 (US); Río Boiauassú, 100 m., *Schultes* 6876 (US).

Hipolito Ruiz describes the location of the pueblo of Puzuzo [sic!] in some detail in Chapter 38 of his *Travels*,²⁶ and I believe he collected subsp. *pozuzoensis* there. In any event there is in the British Museum (Nat. Hist.) a sheet labeled in Pavon's (?) hand “*Vismia* sp. nova del Peru,” from the herbarium of Lambert, who acquired the Ruiz and Pavon collection. It is a good example of this subspecies.

²⁶ Cf. Field Mus. Publ. Bot. 21:172–183. 1940.

20. *Vismia plicatifolia* Hochr. Ann. Cons. Jard. Genève 21: 54. 1919.

Caopia parvifolia Rusby, Phytologia 1: 65. 1934. TYPE: Chuquini, Cordillera Real, 900 m., Bolivia, 17–19 April 1926, *Tate* 1128 (NY).

TYPE: Polo-Polo near Coroico, North Yungas, Bolivia, *Buchtien* 222 (G, Holotype, Photo FM 9169, from B; isotypes, C, E, F). Paratypes: Yungas, *Bang* 595 (C, E, F, G, K, L, US).

ADDITIONAL SPECIMENS EXAMINED:

BOLIVIA: Without locality, *Bang* 2933²⁷ (K, US). Coroico, North Yungas, 2000 m., *Mexia* 4268 (MO, UC); Polo-Polo, near Coroico, *Buchtien* 6014 (US); Yungas, 1800 m., *Rusby* 720 (F, K, US), *Bang* 621 (US); San Francisco, *Werdermann* 2525 (Photo FM 9159 of specimen B); Hacienda Simaco, on road to Tipuani, 1400 m., *Buchtien* 5464 (MO, S, US); Ixiamas (Isiamas), 240 m., *Cárdenas* 1947 (K, NY, US), *White* 1149 (US); Milluhuaya, south of Coripata, 1300 m., *Buchtien* 4645 (US); Songo, *Bang* 835 (BM, E, G, K, US); San José, 1500 m., *R. S. Williams* 385 (K, US); Buena Vista, Santa Cruz, 450 m., *Steinbach* 5081 (NY), 6519 (BM, F, K), 7252 (BM, E, K, MO, U, UC); Yungas de San Mateo, *Steinbach* 8403 p.p. (F, K, US); Riberalta, Beni, 300 m., *Cárdenas* 4172 (US).

PERU: SAN MARTÍN: San Roque, *L. Williams* 7043 p.p. (F).

The type of *Caopia parvifolia* has small, hardly plicate leaves, unusual for this species, and weaker, more delicate panicles. Tate's collection is unique, but another collection, *Steinbach* 6519, is transitional to the typical phase. This Bolivian collection from Santa Cruz comes from a lower elevation than the Tate specimen. However a second Steinbach collection (no. 7252) from the same locality is more nearly typical. In short, *C. parvifolia* can hardly represent more than the normal variation to be expected within a species.

Certain Peruvian collections prove difficult to place, showing characters of both *Vismia sprucei* and *V. cayennensis*, as well as *V. plicatifolia*. These include: Puerto Bermúdez, Junín, 375 m., *Killip & Smith* 26439 (US) and Pumayacu, Loreto, 600–1200 m., *Klug* 3140 (US; but no. 3140 at A and MO is *V. glabra*).

21. *Vismia viridiflora* Duchass. ex Triana & Planch. Ann Sci. Nat. IV. Bot. 17: 302. 1862.

Caopia viridiflora Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: Panama, *Duchassaing* (likely from the vicinity of Panama City; cf. Contr. U.S. Nat. Herb. 27: 44). Paratype: Chagres, on Chagres River [now Canal Zone], Feb. 9, 1850, *Fendler* 6 (K, OXF, TCD, US).

ADDITIONAL SPECIMENS EXAMINED:

PANAMA: Without locality, *Seemann* 466 (BM, K, S); Campana, 600–800 m., *Allen* 1692 (NY, US); Matachin, *Hayes* 456 (NY); Ancón Hill, 180 m., *R. S. Williams* 7 (NY, US); Bismarck, above Penonome, *R. S. Williams* 559 (NY, US). CANAL ZONE: Bohio, 10–20 m., *Maxon* 4774 (S, US); Chiva-Chiva Trail, *Piper* 5763 (S, US); Río Tapia, *Standley* 30688 (K, US); Chagres, *Fendler* 299 (K).

COLOMBIA: CHOCÓ: Cordillera Occidental, 1200 m., *Triana* (P).

Vismia viridiflora has the general appearance of *V. cayennensis*, from which it differs in its fine, almost microscopic puberulence on

²⁷ No locality data supplied by account in Bull. N.Y. Bot. Gard. 4:327. 1907.

the lower surfaces of the more narrowly lanceolate leaves. The other distinguishing characters mentioned by Triana and Planchon, and illustrated by *Fendler* 6 from Panama, are minor and without taxonomic significance.

22. *Vismia lehmannii* Hieron. Bot. Jahrb. Engler 20, Beibl. 49:53. 1895.

Caopia lehmannii Hieron. loc. cit.

TYPE: Vicinity of Popayán, Department of Cauca, Colombia, 1750 m., *Lehmann* 3551 (isotypes BM, K, US).

ADDITIONAL SPECIMENS EXAMINED:

COLOMBIA: CAUCA: Popayán, *Lehmann* K74 (probably part of type collection) (K, S, US), BT1086 (A, K, L); Capilla, *Lehmann* BT450 (L). EL VALLE: Piedra de Moler, Rio Digua, 900–1180 m., *Cuatrecasas* 14893 (US). CAQUETÁ: Florencia, 420 m., "lacre," *Pérez-Arbeláez* 692 (US).

Vismia lehmannii is more closely related to *V. baccifera* than to *V. cayennensis*, contrary to the opinion of Hieronymus. The leaves are nearly farinose-puberulent, recalling the vestiture of *V. confertiflora* Spruce, although smaller than those of that species. From forms of *V. baccifera* growing in the Popayan region, this local species may be identified by the small flowers crowded in a compact panicle.

23. *Vismia cuatrecasasii* Ewan, sp. nov.

Arbor gracilis 20 m. alta, ramis ad 25 cm. diam., castaneis, internodiis superioribus aliquantum brevibus, 5–7 cm. longis; laminis foliorum magnis, ovatis vel oblongo-ovatis, ad basim rotundatis, 12–20 cm. longis, 7–10.5 cm. latis, cuspidatis, supra vitreo-viridibus, glabris, infra puberulentis, sparse atro-punctatis vel eglandulosis, prominente venosis, coriaceis, atque flexilibus, siccitate submembranaceis, omnibus breviter petiolatis, petiolis subalatis, 5–12 mm. longis; paniculis oblongo-pyramidalibus, cum adjunctis ramis in axillis superiorum foliorum, rache atque pedicellis rufo-puberulentis; calycibus subcampanulatis, submembranaceis, minute tomentulosi, pruinosis, sepalis ovatis, acutis, 8–9 mm. longis, divaricatis, interdum paullo atro-pustulato-glandulosis in margine, marginibus hyalinis atque subobsoletis; petalis lanceolato-ovatis, obtusis, ochroleucis, extus subtiliter atro-lineatis, apice sparse vittatis, intus dense tomentosis, 11–16 mm. longis; fasciculis staminorum quinque omnibus dense comosis, apice ramosis.

Slender tree up to 20 m. high, the stems to 25 cm. in diameter, the bark brown scaly, the upper internodes rather short, 5–7 cm. long; leaves large, leathery and flexible when fresh, thinner when dried, all shortly petiolate, the petioles 5–12 mm. long, more or less wing-margined or channeled above, the blades ovate to oblong-ovate, rounded at the base, 12–20 cm. long, 7–10.5 cm. wide, abruptly acute at apex, the upper surfaces bright lustrous green when fresh, rather dull in the herbarium, glabrous, the lower surface finely puberulent,

weakly punctate with black dot-like glands or at times evidently without glands, the midrib and secondary veins distinct and wholly anastomosing in submarginal loops; panicle oblong-pyramidal, at times with supplementary lateral branches in axils of the uppermost leaves, the rachises and pedicels rufous-puberulent; calyx subcamp-anulate, thin-textured and early withering, finely but unevenly tomentulose, more or less pruinose, the sepals ovate, acute, 8–9 mm. long, spreading, sometimes with a few black pustulate glands on the margins, the hyaline margin nearly obsolete; petals lance-ovate to narrowly lanceolate, obtuse, cream-colored, finely lineate with black pencil markings on outside, weakly vittate toward the summits, densely tomentose within, 11–16 mm. long; stamen columns 5, all densely comose, branching about midway into several branches; fruit unknown.

Type in the U.S. National Herbarium, no. 1,950,013, collected between La Herradura de Ordóñez and Peña de Campotraste, Río Calima (region of Chocó), Department of El Valle, Colombia, alt. 5–10 meters, 3 March 1944, by José Cuatrecasas (no. 16687); isotype in the herbarium of Tulane University.

PARATYPES:

COLOMBIA: EL VALLE: (Costa del Pacifico): Barco, Río Cajambre, 5–80 m., *Cuatrecasas* 17199 (NO, US); between Isla de Golondro and La Amargura, Río Yurumanguí, 10–40 m., *Cuatrecasas* 16049 (US); Puerto Merizalde, Río Naya, 5–20 m., *Cuatrecasas* 13954 (US); Silva, Río Cajambre, 5–80 m., *Cuatrecasas* 17641 (US); Quebrada de Guapecito, Río Cajambre, 0–5 m., *Cuatrecasas* 17694 (US).

Vismia cuatrecasasii is evidently restricted to the lowland rain forests of the Pacific Coast of Colombia. The collections at hand, all made by Dr. José Cuatrecasas, are very uniform for the genus. The taxonomic position of this species is clearly with *V. obtusa* of Ecuador and Peru, from which it is at once separable by its larger flowers. From the form of *V. lauriformis* that grows in the same region, this species may be distinguished by the darker red tint of the lower leaf surface, the pubescence obscuring the secondaries, whereas the dark-colored veins in *V. lauriformis* contrast prominently with the red-brown pubescence.

The distinguished botanist, José Cuatrecasas, is commemorated in the name of this *Vismia*; he has made the largest and most critical collections not only of *Vismia* but of the rich Colombian flora in general.

24. *Vismia baccifera* (L.) Triana & Planch. Ann Sci. Nat. IV, Bot. 17: 298. 1862.
Hypericum bacciferum L. Mant. 277. 1771.

Vismia guttifera Pers. Syn. Pl. 2: 86. 1807. Based on *Hypericum bacciferum* L. An illegitimate renaming.

Caopia baccifera Kuntze, Rev. Gen. Pl. 1: 58. 1891.

TYPE: Said to be from Mexico, collected by J. C. Mutis, but undoubtedly from Colombia and likely from the vicinity of Mariquita, where Mutis lived and worked.

There is an authentic Mutis collection in the U.S. National Herbarium (sheet no. 1,561,386) and another from Lambert's Herbarium now in the British Museum (Natural History). Eyma reported in 1932 that no type exists in the herbarium of the Linnaean Society, London.

Vismia baccifera is the most polymorphic species of the genus. Typical plants, which are trees of Colombia, are here associated with three subspecies, each with a more or less consistent geographic range but commonly connected by a series of morphologically transitional forms that prove difficult to separate.

Key to the Subspecies

Leaves strongly bicolored, white-tomentulose beneath, bright lively green above, generally broadly deltoid-ovate or at times ovate or lance-ovate.

V. baccifera* subsp. *dealbata

Leaves not strongly bicolored white and green, more or less ferruginous or unevenly cinereous or canescent beneath, usually dull dark green above, varying from cordate-ovate or suborbicular to ovate or even lanceolate, seldom exactly broadly deltoid-ovate.

Leaves ferruginous-tomentulose beneath, lance-ovate, acuminate to an acute narrow apex, rounded or often subcordate at the base, the principal blades averaging 14–18 cm. long; petioles often 2 cm. long or more; lowland and middle elevations of Venezuela, Colombia, and Panama.

V. baccifera* subsp. *ferruginea

Leaves not ferruginous-tomentulose beneath, varying from cinereous to ochre-yellow sometimes on same branchlet, chiefly broadly ovate but variable, generally not lanceolate, if the principal blades as much as 14 cm. long then proportionately broader; petioles less than 2 cm. long; interior and upland Andes from Colombia to Bolivia.

Petals short, 7–9 mm. long; fruiting panicle rather compact, the branches short, stout; Peru and Bolivia. . . . ***V. baccifera* subsp. *subcuneata***

Petals longer, 10 mm. long or more; fruiting panicle diffuse, the branches spreading, slender; Colombia and northern Ecuador.

V. baccifera* subsp. *baccifera

24a. *Vismia baccifera* subsp. *baccifera*.

SPECIMENS EXAMINED:

COLOMBIA: NORTE DE SANTANDER: Hoya del Río Margua, Quebrada del Río Negro, region of Sarare, 1200–1300 m., *Cuatrecasas* 12932 (US). CUNDINAMARCA: Between Cachipay and Quebrada del Hueso, 1600–1700 m., *Cuatrecasas* 13591 (US); 11 km. south of La Palma, 1950 m., *Little* 7392 (NA, NO). ANTIOQUIA: Angelopolis, 1950 m., *Gutierrez & Barkley* 17C679 (US). CHOCÓ: Nuquí, *Romero C.* 418 (US). EL VALLE: Below Queremal, Río San Juan, Hoya del Río Digua, 1300–1500 m., *Cuatrecasas* 23868 (US); Córdoba, *Killip* 5079 (NY, US). CAUCA: La Capilla, 25 km. n. of Popayán, 1740 m., *Killip* 38469 (US); "Las Guacas," Morales, 1600–1650 m., *Pennell & Killip* 6298 (US).

The typical tree of Colombia has broadly ovate rather long-petiole leaves, that are not strongly bifacial, but have a pale yellowish or ashy lower surface, a diffuse panicle whose branches are spreading at right angles to its rachis, moderately large flowers with white petals, about half again as long as the sepals, the sepals with a prominent

membranous flange, and baccate fruits. It is these large (12–13 mm. in diameter, 15–17 mm. long), heavy fruits that must have suggested the original specific name “baccifera” to Linnaeus, who, indeed, may have received the manuscript name from Mutis.

There is a fragmentary collection in the Chicago Museum of Natural History Herbarium (no. 940,497) bearing two labels, one a form label provided by the Museum d'Histoire Naturelle, Paris, and a second more important ticket which bears the characteristic mark of the Willdenovian Herbarium at Berlin and the words “*Hyperic[um] bacciferum* [vol.] 3 p. 1440.” The pagination refers to Willdenow's *Species Plantarum*. The leaves of this collection, though fragmentary, are a remarkably close match for some of the leaves accompanying Mutis 3718 (US 1,563,038), an authentic sheet of *Vismia baccifera*. It is possible that this incompletely labeled collection from Bonpland's herbarium may represent portions of the Mutis material.

24b. *Vismia baccifera* subsp. *dealbata* (H.B.K.) Ewan, comb. nov.

V. dealbata H. B. K. Nov. Gen. & Sp. 5:184. t. 454. 1822.

Caopia dealbata Kuntze, Rev. Gen. Pl. 1: 59. 1891.

V. hamanii Blake, Contr. Gray Herb. 53: 41. 1918. Type: San Félix-Táchira, Táchira, Venezuela, 16 May 1917, “lancetillo,” *H. M. Curran* & *M. Haman* 1010 (GH; isotypes, A, K, NY, P, US, WU). The label of an isotype reads, “Estación Táchira,” which is a pueblo in the Río Táchira valley; “San Félix” has not been located in the State of Táchira; it was transcribed by Blake as “San Felipe.”

TYPE: Labeled “No. 1152. Rio Negro. Cassiquiare” from Río Negro and Río Cassiquiare, Venezuela, *Humboldt & Bonpland* (P, Killip photo 714).

ADDITIONAL SPECIMENS EXAMINED:

SURINAM: Forest of Zandery, 31 May 1916, *Samuels* (US), 275 (P).

FRENCH GUIANA: Without locality, in 1792, *Leblond* (BM); Maroni, in 1862, *Melinon* (E, US); Cayenne, *Jelski* (K, P, US).

VENEZUELA: ANZOÁTEGUI: Cerro Peonia (Cerro Coroy), northeast of Bergantín, *Steyermark* 61394 (F). CARABOBO: Buenavista, *Linden* 1502 (FI, G). DISTR. FEDERAL: Without locality, *Birschel* (TCD); Caracas, 1400 m., *Pittier* 9184 (US); El Junquito, 1500 m., *Lasser* 1122 (US); between Caracas and La Guaira, 1100–1300 m., *Pittier* 9558 (NY, US); between La Guaira and Río Grande, “onotillo,” *Curran & Haman* 985 (paratype of *V. hamanii*) (A, US). MÉRIDA: Tabay, 1900–2200 m., “punta de lanza,” *Gehriger* 351 (MO, US); Los Teques, 1140 m., *Eggers* 13031 (US); Capellania, 1600 m., “lancetillo,” *Tamayo* 2436 (UC, US); Mérida, 1700 m., *Pittier* 12748 (G, US); along Río Albarregas, Monte Serpa, 1675–2135 m., “mancha ropa,” *Steyermark* 55934 (US). TÁCHIRA: Alto de Lirio, between Bramón and Las Delicias, 1890–2285 m., *Steyermark* 57440 (US). TRUJILLO: “Andes de Truxillo,” *Linden* 332 (P).

COLOMBIA: ANTIOQUÍA: Fredonia, *Toro* 1037 (NY). BOYACÁ: La Chapón, 1050 m., *Lawrance* 303 (K, MO). CAQUETÁ: Solano, near Tres Esquinas, 200 m., “lacre,” *Little & Little* 9501 (transitional to subsp. *ferruginea*) (NO, US). CUNDINAMARCA: 10 km. south of Gachalá, 2150 m., *Fosberg & Grant* 21966 (NO, US); Finca “La Esmeralda,” Vereda Tórriba, San Francisco, 1550 m., “punta de lanza,” *García-Barriga* 10989 (US); near Sasaima, 1600–1800 m., *Cuatrecasas* 9632 (US); between El Salto and El Colegio, 1680 m., *Cuatrecasas*

8242 (US); above El Colegio, 1500–1600 m., *Dugand* 3688 (US); Estación Santana, 1600–1700 m., *Dugand & Jaramillo* 3977 (US); between Sueva and Gachetá, 1800–2100 m., *Cuatrecasas & Jaramillo* 11991 (US). HUILA: Santa Ana, alt. 1650 m., “lacre, small tree to 8 m., 10 cm. D.B.H., bark gray, slightly fissured; flowers brown; produces mucilage for sealing letters; fruit produces red coloring, and also medicine for livestock, common in dry forest,” *Little & Little* 7110 (NO, US). MAGDALENA: Río Hacha, *Purdie* (K); around San Andrés de la Sierra, western slope of Sierra de Santa Marta, 1100–1300 m., *Pittier* 1651 (US); Santa Marta, *Purdie* (TCD), 600 m. *H. H. Smith* 803 (K, MO, UC, US). META: Puerto López, *Fosberg* 20173 (NA, NO), *Little & Little* 8273 (NO, US); Villavicencio, toward El Parrao, 500 m., *Cuatrecasas* 4568 (US); Cabuyaro, Los Llanos, Río Meta, 235 m., *Cuatrecasas* 3593 (US); Cano Ciervo, Sierra de la Macarena, 600 m., *Philipson et al.* 2092 (BM, US); along Río Ocoa, southeast of Villavicencio, 500 m., *Killip* 34381 (US). NORTE DE SANTANDER: Toledo, 1700–1900 m., *Killip & Smith* 20037 (US); Río Pamplonita, between Cúcuta and Pamplona, 700 m., *Cuatrecasas & García-Barriga* 10177 (US). SANTANDER: Charta, 2000–2600 m., *Killip & Smith* 19232 (US); Bucaramanga, 1000 m., *Weir* 93 (K), “sangrito,” *Killip & Smith* 16335 (NY, US); 10 km. north of Bucaramanga, 1500 m., *Araque-Molina & Barkley* 18S215 (US); 18 km. south of Socorro, 1200 m., *St. John* 20540 (NO, US); Mesa de los Santos, 1500 m., *Killip & Smith* 15074 (US). TOLIMA: Líbano, 1100–1300 m., *Pennell* 3446 (NY, US).

BRAZIL: PARÁ: Santarém, May 1850, *Spruce* (BM, E, FI, K, OXF), *Spruce* 766 (K).

This subspecies *dealbata* has long been treated as a full species perhaps because of the rather striking whitish lower leaf-surface but a study of a large series of specimens shows this tree of Venezuela and northern Colombia with strongly bicolored leaves to be a variable geographic population of the widespread *Vismia baccifera*. The number of intermediate specimens that cannot be assigned to the subspecies or the typical *baccifera* is too large to regard this subspecies as distinct from *V. baccifera*.

There is a notable collection in the Harvey Herbarium of the Dudley Herbarium, Stanford University, with a ticket reading “*Vismia guianensis*, Pers. DC. 5, Porto Rico, 1844.” which is in fact this subspecies *dealbata*. No *Vismia* is known from the island of Puerto Rico and I find no record of botanical collections having been made on the island during the year 1844. The specimen matches collections of this subspecies from coastal localities in Venezuela. Henrik Johannes Krebs botanized in Puerto Rico, according to Urban, and traveled on occasion to both North and South America. Though Urban is not detailed in his dates, Krebs’ period of activity supports the conjecture that this specimen was taken, not in Puerto Rico, but at a Venezuelan port on one of these trips. Duplicates of this collection are preserved at Dublin and at Geneva (ex Delessert Herbarium).

The type of *Vismia dealbata* H.B.K. at Paris does not closely resemble the illustration of the species (*Pl.* 454) accompanying the original description. Perhaps the artist somewhat idealized the plant for purposes of illustration, but the leaves are drawn as being more or less undulate, apparently of a firm, thick texture, and tending to fold along the midrib, whereas the type shows a plant with plane leaf-blades of a thin or membranous texture, at least as preserved in the herbarium. However, the leaves are described as "integerrima," which conforms with the type. The word "subcoriacea" might be interpreted as fortifying the artist's figure, yet I believe that a firm, cutinized leaf surface is intended, in spite of the evidently thin texture of the type specimen. In interpreting the species as distinguished from its close relatives the phrase "subtus pilis stellulatis tenuissime albido-tomentosa," descriptive of the white-tomentose character of the leaves, is important.

24c. *Vismia baccifera* subsp. *ferruginea* (H. B. K.) Ewan, comb. nov.

V. ferruginea H. B. K., *Nov. Gen. & Sp.* 5: 183. 1821.

Hypericum cuspidatum Willd. ex Spreng. *Syst. Veg.* 3: 351. 1826, *pro syn. V. ferrugineae*.

V. cuspidata Steud. *Nom. Bot.*, ed. 2, 1: 787. 1840, *nom. nud.* Based on *H. cuspidatum* Willd.

Caopia ferruginea Kuntze, *Rev. Gen. Pl.* 1: 59. 1891.

TYPE: Orinoco River, between Atures and Maypures, in the present state of Bolívar, Venezuela, *Humboldt & Bonpland s.n.* (Humboldt & Bonpland Herbarium P, Killip photo 713).

ADDITIONAL SPECIMENS EXAMINED:

VENEZUELA: Forests of Guamita, "cedrillo," *Delgado* 132 (US). **CARABOBO:** Near Tinaquielo, *Chardon* 137 (US). **AMAZONAS:** Esmeralda, 143 m., *L. Williams* 15375 (US). **BOLÍVAR:** Guayapo, 100 m., *L. Williams* 11754 p.p. (K); La Union, Medio Caurá River, 120 m., *L. Williams* 11689 (US).

COLOMBIA: **ANTIOQUIA:** Salto de Guadalupe, 1600 m., *Hodge* 6964 (US); Llano Grande, near Río Negro, 2200 m., *Daniel* 3850 (US); Angostura, 2000 m., *Fosberg* 21604 (NO); Angelópolis, 1950 m., *Gutierrez & Barkley* 17C680 (US); Fredonia, *Toro* 187 (NY); Primavera, Medellín, 1560 m., Oct. 1945, *Ruiz* (US); Palmitas, 1700 m., *Scolnik et al.* 532 (US). **BOLÍVAR:** San Martín de Loba, *Curran* 183 (US). **BOYACÁ:** Between Moniquirá and Arcabuco, 2150 m., *Pérez-Arbeláez & Cuatrecasas* 8168a (US). **CAUCA:** 4 km. north of Popayán, 1680 m., *Ewan* 15860 (NO, US); "El Ramal" to Río Sucio, west of Popayán, 1600–1900 m., "a tree in prairie, petals white," *Pennell & Killip* 8146 (NY, US). **CHOCÓ:** Río Atrato, near Quibdó, 400 m., *Araque-Molina & Barkley* 19ChO47 (NO, US); between Oveja and Quibdó, *Archer* 1741 (NY, US); Istmina, Río San Juan, 75 m., *Killip* 35455 (BM, S, US); banks of Quebrada Togoromá, *Killip & Cuatrecasas* 39090 (K, US). **CUNDINAMARCA:** Fusagasugá, *André* 1411 (NY); Buenavista to Pipiral, southeast of Quetame, 1000–1200 m., "lacre," *Pennell* 1674 (US). **HUILA:** 30 km. northwest of Palermo, 2100 m., *Little* 8727 (NO, US); drainage of Quebrada de la Cuandinosa, 15–20 km. east of Gigante, 1500 m., *Fosberg* 19851 (NO, US). **META:** Susumuco to Villavicencio, *Triana* 12 (BM). **SANTANDER:** Quebrada Angulo, 4 km. south of Lebrija, 955 m., "manchador," *St. John* 20588 (NO, US). **EL VALLE:** Alto de las Brisas, Pichindé, Hoya del Río

Cali, 2050–2100 m., *Cuatrecasas* 18331 (US); Alto de Miravalle, Pichindé, 2020–2080 m., *Cuatrecasas* 18327 (US).

The rich red-brown lower surface of the leaves of this subspecies is the first feature to attract attention. The leaf-blades vary widely from long-acuminate to shortly ovate; they are not usually as distinctly truncate at the base as those of subsp. *dealbata*. This subspecies is frequent in Colombia and in transmontane Venezuela.

24d. *Vismia baccifera* subsp. *subcuneata* (Huber) Ewan, comb. nov.

V. subcuneata Huber, Bol. Mus. Goeldi 4: 588. 1906.

TYPE: "Quebrada grande do Cerro de Canchahuaya," basin of Río Ucayali, Junín, Peru, Nov. 13, 1898, *Huber* 1479.

SPECIMENS EXAMINED:

PERU: JUNÍN: Middle Uca Yali, *Tessmann* 3279 (G, NY, S); Schunke Hacienda, above San Ramón, 1300–1700 m., *Schunke* A103 (US); Pichis Trail, Porvenir, 1500–1900 m., *Killip & Smith* 25911 (F, NY, US). SAN MARTÍN: Tingo María, 800 m. *Allard* 21629 (US). San Carlos, *Mathews* 1309 (CGE, GL, K); Moyobamba, *Mathews* 1311 p.p. (CGE).

BOLIVIA: Charopampa, 570 m., Nov. 1907, *Buchtien* 1907 (L, US); San Carlos, 850 m., *Buchtien* 889 (F, US), 890 (US), 890a (US), 750 m., 9 Nov. 1907, *Buchtien* 2114 (US), 750 m., 11 Sept. 1907, *Buchtien* 2114 p.p. (K, US); Mapiri, *Rusby* 1810 p.p. (US); Sorata, *Bang* 1724 p.p. (US), 850 m., 16 Dec. 1926, *Buchtien* (US); Tumupasa, *R. S. Williams* 339 (K, NY, US), 517 (K), 547 (K, NY); Río Chimate, 570 m., *Tate* 545 (NY).

This subspecies is separated geographically from the other components of *Vismia baccifera*, being restricted to Peru and Bolivia, and is the most distinct morphologically of its subspecies. The leaves resemble subsp. *dealbata* at times in being somewhat bifacial but less uniformly cinereous, and oblong rather than deltoid. The crowded panicle is perhaps the most striking difference from other subspecies of *V. baccifera*, but in this regard the collections are not uniform and the lack of other distinctive characters leads me to conclude that like the other taxa of *V. baccifera* this subspecies is a recent variation maintained especially by geographic isolation.

25. *Vismia lauriformis* (Lam.) Choisy, Prodr. Monog. Hyper. 35. 1821.

Hypericum petiolatum L. f. Suppl. Plant. 345. 1781; non *H. petiolatum* L. (1764).

H. lauriforme Lam. Encycl. 4: 152. 1789. Renaming of *H. petiolatum* L. f. (1781) non L. (1764).

H. arboreum J. F. Gmel. in L. Syst. Nat., ed. 13, 2: 1156. 1792. A renaming of *H. petiolatum* L. f. (1781) non L. (1764). Illegitimate.

H. laurifolium Willd. Sp. Pl. 3: 1440. 1803. A renaming of *H. petiolatum* L. f. (1781) non L. (1764). Illegitimate.

Vismia laurifolia Pers. Syn. Pl. 2: 86. 1806. A renaming of *Hypericum lauriforme* Lam. Illegitimate.

H. sanguineum L. ex Triana & Planch. Ann. Sci. Nat. IV, Bot. 17: 301. 1862. A manuscript name "fide specim. authentici Mutisiani in herb. Linn," now in Herb. Linnaean Soc., London.

Caopia lauriformis Kuntze, Rev. Gen. Pl. 1: 59. 1891.

V. calvenscens Gilg & Hieron. Bot. Jahrb. Engler 21: 322. 1895. TYPE: Vicinity of Popayán, Department of Cauca, Colombia, *Stuebel* 259. Presumably lost at Berlin.

TYPE: "Nova Granada," i.e. Colombia, communicated by José Celestino Mutis (authentic coll. US 1,562,666). The type was taken most probably in the Department of Cundinamarca. The fruit was described by Linnaeus *filius*, but the US sheet is only in early flower, and so it is doubtful if that represents an exact duplicate of the collection in the Linnaean Herbarium.

ADDITIONAL SPECIMENS EXAMINED:

FRENCH GUIANA: Maroni, 1864, *Melinon* (NY); Cayenne, in 1839(?), *Leprieur* (F).

VENEZUELA: BOLÍVAR: Roraima, *Schomburgk* 861 (BM, G, NY, P), 552 (FI, G, P); along mesa escarpment between Santa Teresita de Kavanayén and wooded quebrada about 8 km. northwest of Kavanayén, 1220 m., *Steyermark* 60481 (US); along Río Karuai, northwest of Santa Teresita de Kavanayén, 1220 m., "minchuba-rei-yek," *Steyermark* 60827 (US); Gran Sabana, between Kun and Uaduara-parú, south of Mount Roraima, 1065–1220 m., *Steyermark* 59091 (US), 59099 (US). ANZOATEGUI: Ijigua, northeast of Bergantín, 600–800 m., "lacre," *Steyermark* 61234 (US). SUCRE: Los Altos, *Tamayo* 2168 (US).

COLOMBIA: META: Villavicencio, *Pennell* 1403 (NY); Apiai, Villavicencio, 500 m., *Cuatrecasas* 4757 (US). ANTIOQUIA: Medellín, *Toro* 757 (NY); Puerto Valdivia, Río Cauca, 240–260 m., *Metcalf & Cuatrecasas*, 30070 (UC, US). NORTE DE SANTANDER: Quebrada de Gibraltar, Río Cubugón, region of Sarare, 320 m., *Cuatrecasas* 13228 (US). SANTANDER: Between Puerto Wilches and Puerto Santos, *Killip & Smith* 14852 (NY, US), 14890 (NY, US). CUNDINAMARCA: La Mesa, 1200 m., *Triana* (K); Guaduas to Palmar (Quebrada Honda), road to Guaduoero, 1040–1150 m., *García-Barriga* 11778 (US). CAUCA: Río Ortega to San Antonio, 1500 m., *Pennell & Killip* 7263 (NY); Popayán, *Lehmann* 2832 (K), 5543 (K). TOLIMA: Líbano, 1100–1300 m., *Pennell* 3446 p.p. (MO). Mariquita, *Humboldt & Bonpland* 1715 (P).

Vismia lauriformis is highly variable over its range and at times is separable from typical *V. baccifera* and its subsp. *dealbata* only with difficulty. The leaves of *V. lauriformis*, however, are generally smaller and glossy above. The acute, at times almost cuneate, leaf-base is an especially useful character for recognition.

In the Popayán region of southern Colombia, Department of Cauca, a peach-leaved form of *Vismia lauriformis* with narrower leaf-blades, often acuminate to a long point in the manner of adult leaves of *Eucalyptus globulus*, more or less replaces the typical tree of the more northern districts of Colombia. This form has never been distinguished nomenclaturally, and it does not seem necessary to do so at this time, but it illustrates again the local endemism of that interesting region. Collections representative of this form include: Popayán, *Lehmann* 2832 (US), 5543 (S, US); La Capilla, 25 km. north of Popayán, 1740 m., *Killip* 38480 (US); Tres Cruces, Popayán, *Yepes, Araque, & Barkley* 18CaO63 (NO, US).

Vismia lauriformis is related both to *V. baccifera* and to *V. guianensis*, especially to *V. baccifera* subsp. *ferruginea*, and through *V. falcata* forms an almost complete phyletic series to *V. guianensis*.

26. *Vismia mandurr* Hieron. Bot. Jahrb. Engler 20, Beibl. 49: 54. 1895.

Caopia mandurr Hieron. loc. cit.

TYPE: Three syntypes were originally cited, *Lehmann* 920, 5593, and 6617, the originals all probably destroyed in Berlin. Lectotype: *Lehmann* 5593 (US); isoelectotype K; the original was without locality; according to *Lehmann's* field-book (US), no. 5593 has the data: "*Vismia mandurr* Hieron. Species of trees up to 15 m. in height, with large, close, nutant crowns. Leaves dark yellow-green, shiny. Flowers brownish yellow-green. Fruit of the size and shape of a sparrow's egg. Colombia. Grows in moderately dense forests on the mountain slopes above Popayán, 1800–2400 m." In the field-book, the data for 6617 (K) are: "*Vismia mandurr* Hieron. Trees up to 12 m. in height with large crowns. Leaves leathery, dark green. Flowers brownish green. Colombia. Grows in the dense forest formations around Paisbamba above Popayán, 1800–2300 m. Flowers in March." No. 920 (not seen) according to Hieronymus had the data: "Crescit in altiplanitie prope urbem Popayán, alt. s. m. 1200–2000 m., mense Augusto florens et fructifera."

ADDITIONAL SPECIMENS EXAMINED:

COLOMBIA: META: Hacienda El Pao, southeast of San Antonio Fortalecillas, 1710 m., *Little* 7982 (NO, US). HUILA: Parque Arquelógico, 3 km. west of San Agustín, 1800 m., *Little* 7617 (NO); San Agustín, *Daniel* 4101 (US); north of Santa Ana, 1800 m., *Little* 7071 (NO, US). EL VALLE: La Laguna, Río Sanquinini, 1250–1400 m., *Cuatrecasas* 15678 (NO, US, rather atypical). CAUCA: Quebrada de Santo Domingo, Río Palo, 2470 m., *Cuatrecasas* 19373 (US); around Huila, Río Paez Valley, 1600–1900 m., *Pittier* 1300 (US); Popayán, *Lehmann* K75 (F, K); Cristalores, 10 km. east of Timbío, 2225 m., *Grant & Drew* 10653 (NO, US); between Aguabonita and Candelaria, Río San José, region of Moscopán, 2280–2350 m., *Cuatrecasas* 23561 (US). NARIÑO: Piedrancha, 1550 m., *Fosberg* 21090 (US).

From this large series mostly of recent collections, made in part by field botanists under the Foreign Economic Administration, it is desirable to draw up an emended description of this endemic *Vismia* of southern Colombia:

Leaves dark yellowish-green, rather densely crowded at the ends of the nodose branchlets, the internodes generally short; leaf-blades elliptic or oval, often very variable as to size on a single shoot, at times punctate beneath, long-petiolate, the petioles about 2 cm. long, rather stout, stellate-tomentose; panicle cymose, compactly short branching; sepals early spreading, narrowly ovate, reflexed in fruit, the hyaline margin distinct but narrow; petals narrowly ovate, greenish glandular dotted above, tomentose within; fruits large, 10–15 mm. long, greenish.

Vismia mandurr is evidently closely related to *V. lauriformis*, and, like *V. panamensis*, probably represents a recent derivative from that

variable polymorphic species. *V. mandurr* displays a large close crown of dark yellowish-green shining leaves, which are at times punctate, more elliptic and longer petiolate than those of *V. lauriformis*. Also, the sepals are more heavily tomentulose than in *V. lauriformis*, and only becoming thinly so in advanced fruit. The usual crowded panicle recalls that other endemic of southern Colombia, *V. lehmannii*, but that species has more numerous and smaller flowers. From the label records *V. mandurr* may become a forest tree 6 to 15 meters high with a D. B. H. of 8 to 30 centimeters. The cinereous leaves give a glaucous appearance in the field and droop on the tree from their long petioles like the leaves of the garden peach.

F. R. Fosberg records an interesting bit of folk-lore for this species from the Department of Nariño to the effect that the tree is said to grow from the dead body of a worm. "The worm shown me was a scarab larva which had a club-shaped fungus growing from it.²⁸ In alternate years the beetle is supposed to emerge, the other years the tree" (label accompanying *Fosberg* 21090).

27. *Vismia guianensis* (Aubl.) Choisy, Prodr. Monog. Hyper. 34. 1821.

Hypericum guianense Aubl. Pl. Guian. 2: 784. t. 311. 1775.

V. caparosa H. B. K. Nov. Gen. & Sp. 5: 182. 1822. TYPE: "In monte Hyguerate, prope Buena Vista Caracasorum," which is in the vicinity of Los Teques, Aragua, Venezuela (cf. Kew Bull. 1925: 302) (Photo FM 9160 of specimen in Berlin Herbarium, bearing the number 676); isotype labeled "676. Caracas prope Buenavista" in Humboldt & Bonpland Herbarium (P).

V. acuminata var. *caparosa* Choisy in DC. Prodr. 1: 543. 1824.

Caopia guianensis Lyons, Plant Names Sci. & Pop. ed. 2, 94. 1907.

TYPE: "Sylvis et pratis Caiennae et Guianae," that is, the island of Cayenne and the mainland of French Guiana. Brazilian references from Maregrav and Piso are cited as well, which are discussed below.

ADDITIONAL SPECIMENS EXAMINED:

TRINIDAD: Caroni North Bank Road, *Britton & Mendelson* 821 (US); Mount Tocuche, *Britton, Hazen, & Mendelson* 1336 (US); Long Stretch, 25-26 mile posts, *Broadway* 6837 (S, US); Blanchisseuse Road, top of Morne Bleu, *Broadway* 6208 (US); Aripo Savanna, *Britton, Broadway, & Hazen* 307 (US); woods at Ganapo, *Eggers* 1380 (US); woods near Omora, *Eggers* 1411 (US); Ganapo, *Eggers* 1078 (P, UC, US).

SURINAM: Sectie O, *B. W.* 159b (NY, US); Forest Reserve, *Lanjouw* 344 (NY); "reg. inter. ad fl. Surinam," *Hostmann & Kappler* 1249 p. p. (S).

FRENCH GUIANA: Godebert, *Wachenheim* 41 (US); Maroni, 1863, *Melinon* (NY, US); Karouany, *Sagot* 64 (P, S); Cayenne, 1838, *Leprieur* (NY).

BRITISH GUIANA: Without locality, *Schomburgk* 607 (FI, OXF); drainage of Takutu River, Kanuku Mountains, 600 m., *A. C. Smith* 3187 (S, US); Kurupukari, Essequibo River, *A. C. Smith* 2158 (MO, S, US); Mount Iramaik-pang, Kanuku Mountains, 975 m., *A. C. Smith* 3653 (US); Malali, Demerara River, *de la Cruz* 2705 (US); Assakatta, Northwest District, *de la Cruz* 4321

²⁸ For a discussion of *Cordyceps*, the "vegetable fly," see John Ramsbottom, *Mushrooms and Toadstools* (London, 1953), 149-153.

(UC, US), 4281 (UC, US); Kamwatta, Pomeroon District, *de la Cruz* 1213 (US); Kamakusa, *Lang* 370 p.p. (NY, US), 337 (NY, US), *de la Cruz* 2760 (US), 2820 (US), 4175 (US); Akyma, Demerara River, above Wismar, *Hitchcock* 17415 (S, US); Kalakoon, junction of Mazaruni and Cuyuni Rivers, *Graham* 147 (US); Kaieteur Falls, Potaro River, *de la Cruz* 4471 (UC, US); Wanama River, *de la Cruz* 3896 (US); bank of Potaro River, Tumatumari, *Gleason* 345 (US); Butukari, *Gleason* 709 (US); upper Demerara River *Jenman* 4279 (US), 6278 (NY); vicinity of Bartica, Essequibo River, *de la Cruz* 2011 (US).

VENEZUELA: SUCRE: Aricagua, vicinity of Cristóbal Colón, *Broadway* 555 (US). BOLÍVAR: Sabañas de Santa Teresa, Santa Elena, Gran Sabaña, *Tamayo* 2804 (US); Paraguara, *Velez* 2389 (US); El Palmar, 300 m., *Cardona* 2113 (US); Cerro Upuima, Caroní, "uadamá," 1300 m., *Cardona* 2244 (US); fields near Río Tirica, Caroní, Guayana, 500 m., *Cardona* 2200 (US).

COLOMBIA: BOLÍVAR: San Martín de Loba, *Curran* 193 (US). META: Villavicencio, 500 m., *Killip* 34340 (US); Puerto López road, near Villavicencio, *Schiefer* 729 (UC, US). CAQUETÁ: Florencia, 400 m., *Cuatrecasas* 8819 (US); 50 km. southeast of Algeciras, Huila, 1650 m., *Little* 7732 (NO, US). ANTIOQUIA: Bocaná, 1900 m., *Araque-Molina et al.* 350 (US); vicinity of Santa Elena, between Medellín and Río Negro, 2500 m., *Barkley et al.* 387 (US); La Ceja, 2430 m., *Johnson & Barkley* 18C770 (US); Guarne, 2500 m., *Gutiérrez V. et al.* 125 (US); Medioluna, 1700 m., *Molina* 15 (US); Boquerón de Medellín, 2500 m., *Barkley et al.* 113 (US); Bello, 1500 m., *Molina* 21 (NO, US); between Medellín and Río Negro, 2500 m., *Killip et al.* 39878 (US).

BRAZIL: AMAZONAS: San Gabriel da Cachoeira, *Spruce* 2170 p.p. (E, G, OXF, S); San Carlos, Río Negro, *Spruce* 3115 p.p. (BM, E, NY, OXF), erroneously cited as "2115" by Reichardt; Santa Izabel, Río Negro, *Black* 48-2421 (NY). PARÁ: Para, Jul.-Aug. 1849, *Spruce* (BM, TCD). PERNAMBUCO: Tapera, *Pickel* 333 (US).

Vismia guianensis is a frequent tree in the Central Cordillera of Antioquia, where it shows certain morphologic differences. The sepals are sparingly tomentulose on the back and at times subglabrous. The leaf-blades are thicker, average broader and more obtuse than the Guiana collections, and the leaves are often crowded on the ends of the branchlets. The sepals are very prominently reflexed in fruit. The flowers are now green, now whitish.

Aublet cited a Marcgrav reference under his *Vismia guianensis* which may not represent that species. Marcgrav's descriptions, often amounting to characterizations of genera rather than of species, are not precise enough to add certainty to the establishment of the species. On geographic grounds there is some question that Marcgrav could, by the known distribution of Brazilian *Vismias*, have encountered *V. guianensis*. However, Aublet's species is sufficiently validated on other grounds so that this discordant Marcgrav element does not vitiate its standing.

The Colombian collections of *Vismia guianensis* from the headwaters of the Meta and east of the Andes are notably different in leaf-shape, being narrower, more acuminate, and more closely set on the branchlets, recalling certain populations of *Vismia lauriformis*. From

their resemblance to leafy shoots of the garden peach this transandean subspecies may be distinguished as:

27a. *Vismia guianensis* subsp. *persicoides* Ewan, subsp. nov.

A *V. guianensi* subsp. *guianensi* laminis foliorum lanceolatis, tenuiter attenuatis, conspicue petiolatis differt.

Type in the herbarium of Tulane University, collected at Soratama, Río Apoporis, between Río Pacoa and Río Kananari, alt. 250 meters, Amazonas-Vaupés, Colombia, 15 June 1951, by Richard Evans Schultes and Isidoro Cabrera (no. 12570) (NO); isotype in the U.S. National Herbarium.

PARATYPES:

COLOMBIA: AMAZONAS-VAUPÉS: Soratama, *Schultes & Cabrera* 12747 (NO, US). META: Flood plain forest of Río Meta, Puerto Lopez, 240 m., *Little & Little* 8281 (NO, US).

This subspecies is recorded as a "small tree" or "Tree 8 m., 12 cm. D. B. H. Bark gray, rough, deeply furrowed. Flowers brownish." The leaves are rusty, a little paler above, with a microscopic puberulence beneath, the areoles very small, epunctate. The petals are long, spatulate, rounded at the tip, and a little black-vittate. The sepals are ciliolate, with a distinct membranous flange.

28. *Vismia cavanillesiana* Cuatrecasas, Rev. Acad. Colomb. Cienc. 7: 47. 1946.

TYPE: "Abajo de Gabinete en la Hoya del Abra de San Andrés," Department of Huila, Colombia, 1900–2100 m., Mar. 24, 1940, collected by José Cuatrecasas (no. 8605) (Isotypes, NY, US).

ADDITIONAL SPECIMENS EXAMINED:

Colombia: Llano de St. Martín, *Karsten* (W). CAUCA: Popayán, 1700 m., *Triana* 2 (BM). CUNDINAMARCA: Fusagasugá, 1500 m., *Triana* 4 (BM). META: "Susumuco et Villavicencio, 400–1000 m." *Triana* (G, K, W).

Vismia cavanillesiana is a remarkable endemic in several respects. The large flowers are almost unique in the genus, the petals being sparingly glandular-dotted on the outside and heavily villous on the inside. The leaves are unusual, by their large oval long-petiolate blades, dark green and glossy above, ferruginous-tomentulose beneath, with all the nerves prominent and raised beneath. In some respects the leaves recall *V. lindeniana* but the leaf characters approach some forms of *V. baccifera* and perhaps *V. cavanillesiana* is most closely related to that species. Certain Colombian collections of *V. tomentosa* (for example, *Sprague* 265, US) approach this species in their leaf characters but the flowers are smaller. The heavily rufous-tomentose sepals ally this *Vismia* with the Brazilian species *Vismia martiana* and *V. magnoliifolia*, as shown in the key, but the floral characters are otherwise very different.

A collection transitional between *Vismia cavanillesiana* and *V. tomentosa* and further discussed under the latter species is *Cuatrecasas* 22276 (US), from above Las Brisas, Monte El Tabor, Department of El Valle, Cordillera Occidental, 1970–2100 m., Colombia.

29. *Vismia tomentosa* Ruiz & Pav. Syst. Veg. Peruv. Chil. 183. 1798.
Caopia tomentosa Kuntze, Rev. Gen. Pl. 1: 59. 1891.

This species, originally inadequately described, may be given an amplified description on the basis of a good series of collections as follows: Slender tree 3 to 10–20 m. high, the trunk 10–140 cm., in diameter breast high, the branchlets slender, the ultimate branchlets finely red-tomentellous, including the rachises of the panicles; leaves typically large, little if at all reduced above, the blades broadly ovate, rarely oblong, rounded to cordate at the base, 15–23 cm. long, typically 10–12.5 cm. wide or less, often only 5–8 cm., rather abruptly acuminate at tip or cuspidate, rich red-brown-tomentellous beneath, speckled with minute simple hairs in addition, dull coppery-brown above, the veins 12 to 16 pairs, extending to the margin and ascending, raised beneath, impressed above, all petiolate, the petioles stout, 1–2.5 cm. long; panicle ample and compound, or small and few-flowered, much shorter than the uppermost leaves, the flowers short-pedicellate, lustrous chocolate-brown; calyx 7–8 mm. long, the sepals felty-tomentose with a well-defined marginal flange, this becoming increasingly evident in fruit, the fruiting sepals spreading or reflexed; petals spatulate-obovate, floccose with curling hairs on the inner face, yellow or pale green, 8–11 mm. long, shining with a silk-like sheen, lineate or vittate; stamens included; fruit ovoid to conical, acute, more or less 5-grooved, 10 mm. long, wine red or dark brown.

TYPE: "Perou," likely from vicinity of either Cuchero or Chinchao, Department of Huánuco. Authentic collections: Moricand Herb. (G, photographed by Macbride, Photo FM 23957), and ex Lambert Herb. (BM, photographed by Morton, Photo 8049), and ex Herb. Hooker (K, ticketed "Chinchao," which is surely a portion of the same plant as represented by the collection at Geneva). Cf. Field Mus. Publ. Bot. 21: 78. 1940.

ADDITIONAL SPECIMENS EXAMINED:

COLOMBIA: PUTUMAYO: Mocoa, about Puerto Viejo, 580–600 m., *Cuatrecasas* 11385 (US). VAUPÉS: Río Kananarí and Cerro Isibukuri, 250 m., *García-Barriga* 13784 (US). AMAZONAS-VAUPÉS: Raudal de Jirijirimo, Río Apaporis, "tin-ká," *Schultes & Cabrera* 14548 (US), 14946 (US); Raudal Yayacopi, Río Apaporis, *Schultes & Cabrera* 15364 (US), 16938 (US); Soratama, Río Apaporis, 250 m., *Schultes & Cabrera* 12728 (US); Jinogojé, Río Apaporis, 210 m., *Schultes & Cabrera* 15669 (US).

ECUADOR: SANTIAGO-ZAMORA: Along Quebrada Achupallas, 2500–2800 m., *Steyermark* 54542 (F, US); trail between Mirador and Pailas, 2010–2255 m., *Steyermark* 54288a (sterile, F, US).

PERU: LORETO: Yurimaguas, Maynas, *Poeppig* 2421 p.p. (G, L, OXF); Florida, Río Putumayo, at mouth of Río Zubineta, 180 m., *Klug* 2263 (A, BM, F, G, K, US); Timbuchi, on Río Nanay, *L. Williams* 966 (F); Moyobamba, *Mathews* 1311 p.p. (CGE, GL); Manfinfa, on upper Río Nanay, *L. Williams* 1144 (F); lower Río Nanay, *L. Williams* 571 (F, US); Lower Río Huallaga, 155–210 m., *L. Williams* 4016 (F), 4231 (F, US), 4953 (F), 5002 (F, US). SAN MARTÍN: Tarapoto, 750 m., *L. Williams* 6104 (F). HUÁNUCO: Cuchero, *Poeppig* 1361 p.p.

(K, P, W); Mirador, between Acomayo and Chanchao, 2400 m., *Mexia* 7760 (BM, K, S, U, UC, US), *Mexia* 04138 (UC). JUNÍN: Tarma, Huacapistana, 1800 m., *Velarde-Nuñez* 781 (US); Huacapistana, 1680 m., *Sandeman* 4510 (K, OXF).

BOLIVIA: LA PAZ: Mapiri, 750 m., *Rusby* 1810 p.p. (F, K).

BRAZIL: AMAZONAS: Municipality São Paulo de Olivença, basin of Belem Creek, *Krukoff* 8728 (A, BM, F, G, MO, S, U, US); Manáus, Cachoeira Grande, *Ule* 8923, 31 May 1936, *Ducke* 206 (F, US), 22 Nov. 1942, *Ducke* 206 (A, MO, S, US). Manáus, Feb.–Mar. 1945, *Froes* (US); Itapumua, Lower Rio Madeira, *Cooper* III (US).

Vismia tomentosa grows in both the high forest or selva back from the rivers and in the montaña along the river banks. Ynes Mexía describes the bark as “gray flaky over cinnamon brown” and the juice as “thick, gummy, and brick-red.” It is evidently a tree that begins flowering when it attains three meters in height and a trunk diameter of ten centimeters. The flowers are variously described as yellow or pale green, and the capsule wine-red.

Both Choisy and A. P. de Candolle relegated *Vismia tomentosa* to the group of dubious species because the description was too brief to be readily identifiable. The original description reads:

“V. foliis ovatis acutis subtus tomentosis, racemis terminalibus.

Flor. Per. et Chil. tom. 5.

Arbor quadriorgyalis

Habitat in *Peruviae* nemoribus versus *Cuchero Chinchao*, *Muña*, *Pozuzo* et *Pillao* ad *Chacahuassi* tractus.

Floret a Julio ad Octobrem.”

The type collection preserved in the Conservatoire botanique de Genève bears a label reading in part “Perou M^{ons}. Pavon. 1827.” This label, added perhaps at the time the material was received by Moricand, is overlaid, however, by what appears to be the smaller original ticket, fortunately preserved, reading “*Vismia tomentosa*. Peru.” That this collection is authentic is corroborated by the fact that the branch is only in bud, a point consistent with Ruiz and Pavon’s having failed to mention floral characters in the original description. Contemporary descriptions of *Vismia* so often included the glands or vestiture of the petals. The characters of the leaves and of the panicle are both well matched by *Cuatrecasas* 11385, from Colombia, and less closely by *Krukoff* 8728 from Brazil. Both of these collections originate in altitudes considerably below that of the type localities.

Actually the collections here referred to *Vismia tomentosa* are not morphologically alike in all their characters. Especially variable are leaf size and texture, and the degree of persistence of the distinctive red-brown tomentum of the under-surface. The collections from the lower Río Huallaga are hardly typical, though this may be due in part to the immaturity of the specimens, in that the leaves are

smaller, narrower, and pale red-brown beneath. All of the collections agree in having terminal panicles (auxiliary panicles present in *Steyermark* 54542), exceeded by the uppermost leaves, and in the singular rich cinnamon-brown-tomentellous lower leaf surface free from glands, the broad almost cordate base and the acute tips of the mature leaves.

Of particular interest is the excellent collection from above Las Brisas, Monte El Tabor, Department of El Valle, Cordillera Occidental, 1970–2100 m., Colombia, made by Cuatrecasas (no. 22276, US), which suggests *Vismia cavanillesiana* in its long-petiolate leaves with prominent impressed nerves and ample many-flowered panicle, but the flowers of this collection are smaller than those of that species and in many respects this collection agrees with *V. tomentosa*.

Of interest are two specimens from central Colombia: San Agustín, Tolima, *Sprague* 265 (BM, K, US), and an immature collection made Sept. 22, 1948, by *A. Gärtner N.*, from between Medellín and Río Negro, Antioquia, 2300–2500 m. (Herb. Fac. Nat. de Agronomía, Medellín).

30. *Vismia billbergiana* Beurl. Vet. Akad. Nya Handl. (Stockholm) 1854: 117. 1856. PLATE 7

Caopia billbergiana Kuntze, Rev. Gen. Pl. 1: 59. 1891.

Evidently a small slender tree or shrub 3 to 6 m. high with almost vinelike branches; leaves of the same size up to the inflorescence, the blades thin-textured, ovate and distinctly apiculate to lanceolate and long-acuminate, the tip 1 cm. long or more, sometimes sub-orbicular, 8–13 (17) cm. long, 5–7 (9) cm. wide, the venation closed, areolate, each areole with a single central dot, bifacial, finely pubescent beneath with light brown hairs, dark green and very sparsely pubescent above with scattered stellate hairs, the petioles short, 1 cm. long; panicle cymose, the flowers small, few, less than 8 in a few-branched terminal raceme; sepals narrowly lanceolate, acute, finely rufous-tomentose, 4–5 mm. long, the flange margin narrow to broad, with a single submarginal black gland; petals lanceolate or narrowly ovate, 9 mm. long, 4 mm. wide, acute or rounded, vittate, comose within; fruit globose, 4–8 mm. long.

TYPE: "In montibus, Porto Bello," Panama, April 1826, by Johan Immanuel Billberg (no. 231) (S, photo NO and US).

ADDITIONAL SPECIMENS EXAMINED:

PANAMA: Fató River, Prov. Colón, 10–100 m, *Pittier* 3876 (C, US); Loma de la Gloria, Prov. Colón, 10–104 m., *Pittier* 4238 (US); Porto Bello, Prov. Colón, 5–100 m., *Pittier* 2437 (US); Frijoles, Canal Zone, *Piper* 5826 (US), *Standley* 27488 (US), 27510 (US); Fish Creek lowlands, Prov. Bocas del Toro, vicinity of Chiriquí Lagoon, *von Wedel* 2383 (US).

Vismia billbergiana is an endemic of Panama recalling *V. sessilifolia* on one hand, and *V. tomentosa* on the other, but certainly more closely

related to the latter. The leaves which are variable (as is frequent in mosaic forming vine shoots) are thinner than those of *V. sessilifolia* and even more prominently apiculate. The cymose panicles are distinctive in this *Vismia*; the inflorescence is inconspicuous since the flowers are both few and small. The apiculate thin-textured leaves and few-flowered racemes recall *V. viridiflora* of Panama and the possibility of hybrid origin between that species and *V. sessilifolia* is suggested. *V. billbergiana* has evidently been overlooked both in the field and in the literature. Standley did not mention the species even in synonymy in considering the Panama flora.

31. *Vismia lindeniana* Dcne. in Turcz., Bull. Soc. Nat. Moscou 31¹: 381. 1858.

LECTOTYPE: Galipan, Venezuela, 1350 m., *Funck & Schlim* 101 (Photo FM 23955, fragment of isotype, F).

ADDITIONAL SPECIMENS EXAMINED:

SURINAM: Forest of Zandery, *Samuels* 275 p.p. (A).

VENEZUELA: Without locality, *Fendler* 41 (US). DISTRITO FEDERAL: Sabañas de Agua Negra, *Pittier* 13785 (US). Matorrales de Agua Negra, 1400 m., *L. Williams* 9939 (US). ANZOÁTEGUI: Quebrada Seca, northeast of Los Chorros, east of Bergantín, *Steyermark* 61528 (F). MONAGAS: Forested summit of mountain northwest of Caripe, 1300–1350 m., “lacre” *Steyermark* 61975 (F, US).

The name “*Vismia lindeniana*” was proposed by Funck, later taken up by Decaisne, and ultimately published by Turczaninow. A collection bearing a label with Funck’s manuscript name has been chosen as the type, although the first cited collection, *Linden* 13, from Cerro de Avila, Province of Caracas, alt. 7000 feet, might well have been designated as the lectotype. However, in choosing types for photographing Macbride and Killip independently selected the Funck and Schlim collection in the Delessert and Paris herbaria respectively.

Vismia lindeniana grows to be a small tree four to six meters high with a trunk as much as twenty centimeters in diameter.

A unique collection made in 1917 in the vicinity of Perija, State of Zulia, Venezuela, *Tejera* 10 (US), with the fruit finely pubescent is possibly teratological for its relatively large fruits, 15–21 mm. long; it is doubtfully referred here. The hirsutulose or strigulose leaves with stiff pustulate-based hairs, are notable, but the shape and the size of the leaves would place it with *Vismia lindeniana*.

32. *Vismia crassa* (Rusby) Blake, Contr. Gray Herb. 53: 41. 1918.

Caopia crassa Rusby, Mem. Torrey Club 4: 204. 1895.

TYPE: Yungas, Bolivia, *Bang* 683 (NY; isotypes, BM, E, F, G, K M, O, US).

ADDITIONAL SPECIMENS EXAMINED:

BOLIVIA: Without locality, *Miers* 178 (BM), *Bang* 2931 (BM, C, E, F, G, S, US, W, WU); Incacorral to Paracti, 2200–2400 m., *Herzog* 2298 (L); Sirupaya, near Yanacachi, South Yungas, 2150 m., *Buchtien* 364 (US); San José, South Yungas, 480 m, *R. S. Williams* 239 (BM, NY).

Vismia crassa is a small tree about four meters high, well marked in the genus for its noticeably thick, firm, ovate leaf-blades, white-lanate beneath, smooth and shining above, borne on stout petioles. This endemic of eastern Bolivia must be allied to *Vismia lindeniana* of cismontane Venezuela.

33. *Vismia martiana* Reich. ex Mart. Fl. Bras. 12¹: 204. t. 37. 1878.

Caopia martiana Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: "Ad urbem Mariana," Prov. Minas Gerais, Brazil, *Martius* (cf. *Martius*, Observ. 890). The sheet in the Munich Herb. bears a number "576" and an annotation in Reichardt's hand (Photo FM 19549). It agrees well with the plate but lacks the flowers illustrated there.

SPECIMENS EXAMINED:

BRAZIL: RIO DE JANEIRO: Therezopolis, *Barreto* 4013 (F); Nova Friburgo, *Glaziou* 12465 p.p. (P); Canto Gallo, *Peckolt* (F, labeled in Reichardt's hand). BAHIA: Ilheos, 1821-1824, *Riedel* (US). MINAS GERAIS: *Langsdorff* (US). CEARÁ: Serra Araripa, Taquara, *von Luetzelburg* 26248A (F). PARÁ: Belterra, *Black* 47-937 (NY).

Vismia martiana has a small congested panicle overtopped by the uppermost leaves which are little reduced and are augmented by leaf-like bracts. The principal leaves are ovate, thick, dull above and felty-tomentose beneath, the punctate dots fainter than suggested by *Martius*'s Plate 37, fig. 15, and the veinlets of the interspaces between the secondaries more obscure. From *V. magnoliifolia* this species differs in its rounded, not acute, leaf-bases, its shorter petioles, 8-12 mm. long rather than 15-20 mm. long, and less ferruginous-tomentose rachises of the panicles. The persistent stigmas of the fruits are conspicuous in both species, and in both the fruiting sepals are spreading. Reichardt contrasted the few-flowered panicle of *V. magnoliifolia* with the many-flowered panicle of *V. martiana*, and the vittate sepals of the former with the evittate sepals of the latter. Neither of these characters, however, are very useful. Only the exceptional specimen of *V. martiana* (for example, *Peckolt s. n.*) shows a many-flowered panicle and *Sello* 1366 (Field Museum photo 9165), cited by Reichardt as *V. magnoliifolia*, displays as many flowers as average specimens of *V. martiana*. The vittate character of the sepals of *V. magnoliifolia* is hardly convincing and at least occasional specimens of *V. martiana* (for example, *Peckolt s. n.*) show dark raised lines on the inner face of the sepals. In short, the two species are indeed closely related and more study of a larger series of collections than I have seen may show that only a single species exists. Nothing is known to me of the ecology of the two *Vismias* in Brazil. Reichardt describes *V. martiana* as becoming a tree whereas *V. magnoliifolia* is a shrub, suggesting from other instances among Andean species that there may be habitat preferences.

34. *Vismia magnoliifolia* Schlecht. & Cham. *Linnaea* 3: 118. 1828 (as "*magnoliaefolia*").

V. hilairii Gardn. ex Hook. *London Journ. Bot.* 2: 334. 1843. TYPE: Serra dos Orgãos, Rio de Janeiro, 900 m., "dry bushy places," January 1837, Brazil, *Gardner* 329 (OXF, isotypes, BM, E, F, FI, G, K, NY, P, S, TCD, US, W).

Caopia magnoliaefolia Kuntze, *Rev. Gen. Pl.* 1: 59. 1891.

TYPE: "Brasilia aequinoctiali," *Sellow* (Photo FM 9165 of specimen in Berlin Herbarium; probable isotypes, K (but lvs. attacked by fungus!), L)

ADDITIONAL SPECIMENS EXAMINED:

BRAZIL: Without locality, *Glaziou* 11804 (BM, C, K, NY, P, US). RIO DE JANEIRO: Serra da Estrella, *Glaziou* 2946 (P). MINAS GERAIS: Lagoa Santa, 9 May 1866, *Warming* (C); without locality, *Langsdorff* (US); Campos, Itacolumi, *Schenck* 3623 (C); Viçosa Agricultural College Grounds, 680 m., *Mexia* 4186 (NY, UC, US), 4373 (NY, U, UC, US); Ouro Preto, *Damazio* 1358 (G); Saramenha, *Macedo* 2740 (US); Gongosoco, Dec. 1834, "a large shrub, full of deep yellow juice similar to gamboge; flowers straw-colored, streaked and speckled with dark red; very common in the coppice woods and on the skirts of the forest," *Bunbury* (CGE).

The relationships of *Vismia magnoliifolia* with *V. martiana* have been discussed under the latter species. When Gardner published *V. hilairii* he correctly removed the plant he was describing from *V. guianensis*, but he did not consider its possible relationships with *V. magnoliifolia*, of which it seems to represent a narrow-leaved form; the long-petiolate leaves with acute bases, and the generally few-flowered panicles are evidences of relationship. Collections of this narrow-leaved form include, in addition to the Gardner type collections:

BRAZIL: Without locality, in 1835, *Riedel* (P); without data, no. 6278 (US), possibly *Glaziou*. RIO DE JANEIRO: Serra dos Orgaos, *Gardner* 321 (CGE); *Wilkes Exped.* (NY, US). MINAS GERAIS: Without locality, *Langsdorff* (US 1,573,893), *Riedel* (US 1,573,615, possibly same source as last, cf. Reichardt); Serra do Caraça, *Claussen* 27 (P).

35. *Vismia reichardtiana* (Kuntze) Ewan, comb. nov.

V. guttifera Salzm. ex Turcz. *Bull. Soc. Nat. Moscou* 31¹: 382. 1858; non Pers. (1807). Syntypes: "Collibus Bahiae," *Salzmann*, *Blanchet* 3041. The Salzmann collection may be designated as lectotype; a duplicate has been examined at E. Duplicates of the syntype *Blanchet* 3041 have been seen at BM, FI, and W. Another collection, *Blanchet* 3520, is cited by Turczaninow as a narrower, more acuminate leaved variant (cf. *V. baccifera* var. *angustifolia* Reich. below).

V. baccifera sensu Reich. in *Mart. Fl. Bras.* 12¹: 204. 1878; non *V. baccifera* (L.) Triana & Planch. (1862). The collections cited as *V. baccifera* by Reichardt are: Bahia, *Salzmann*, *Lhotzky*; Rio das Contas, *Martius*; Ilheos, Jacobina, and Moritiba, *Blanchet* 990, 1863, 3041, 3520; Piaui, *Gardner* 2491; Surinam, *Wullschlaegel*.

V. baccifera var. *angustifolia* Reich. loc. cit. No specimens were referred to the variety as distinguished from the species in original publication. Lectotype: Jacobina, Bahia, Brazil, *Blanchet* 3520 (an authentic sheet

labeled var. *angustifolia* by Reichardt in Herb. Delessert, G.) (Isolectotypes: BM, F, FI, G, P, W).

Caopia reichardtiana Kuntze, Rev. Gen. Pl. 1: 59. 1891. Based on *V. baccifera* sensu Reich. non *V. baccifera* (L.) Triana & Planch.

V. cearensis Huber, Bull. Herb. Boiss. II, 1: 313. (28 Feb.) 1901. Type: Between Fortaleza and Bemfica, Ceará, Brazil, Huber 92 (Boissier Herb. G).

V. guaramirangae Huber, loc. cit. Type: Guaramiranga, Serra de Baturité, Ceará, Brazil, alt. ca. 700 m., Huber 263 (Boissier Herb. G). Topotype: 25 July 1908, Ducke 21274 (Photo FM 9163, of specimen in Berlin Herbarium).

TYPE: No type cited by Kuntze; all the specimens cited as *baccifera* by Reichardt are thus syntypes. As lectotype may be selected: *Gardner* 2491 (US), from Flores, banks of Rio Gurgea, South Piauí, Brazil, August 1839; isoelectotypes: BM, CGE, E, F, FI, G, K, NY, OXF, P, W.

ADDITIONAL SPECIMENS EXAMINED:

BRAZIL: PARÁ: Vicinity of Pará, *Baker* 172 (BM, E, G, L, P, S, W); Belém, *Schultes* 8671 (US), *Silva* 162 (US); Thomé Assú, Distr. Acará, 50 m., *Mexia* 5981 (CAS, G, MO, P, S, U, UC, US), 5988 (US); Garupá, Rio Amazonas, *Killip & Smith* 30579 (NY, US); Island of Marajó, *Kauffman* 7 (US). CEARÁ: Baturité, *Loefgren* 91 (S); near Fortaleza, *Ule* 9071 (F, K, L, US); Serra de Ibiapaba, Campo Grande, *Dahlgren* 965 (narrow-leaved form, F). PERNAMBUCO: Without locality, *Gardner* 939 (BM, CGE, E, FI, NY, OXF, P, S, US), 946 (GL). BAHIA: Without locality, *Bondar* 3017 (F), *Blanchet* 595 (NY); Ilha de Cal, "capianga," *Curran* 107 (US); Maranhas, *Salzmann* 234 (CGE). RIO DE JANEIRO: Porto d'Estrella, *Sellow* 185 (L, UC).

Vismia reichardtiana in its typical form is a shrub four to six meters high of the State of Ceará with shiny, stiff, lanceolate leaves; it is well exemplified by *Ule* 9071 from that state. The extreme leaf form is the narrowly lanceolate *V. baccifera* var. *angustifolia* Reich., well illustrated by *Dahlgren* 965, also from Ceará. This may prove to be but a developmental state of the species when more ample collections are available.

Vismia guttifera Salzm. (1858) is a clearly identifiable name for this species, but is invalidated by an earlier use of the same epithet by Persoon (1807).

The morphological distinctions between *Vismia reichardtiana* and *V. pentagyna* are indicated under the treatment of the latter. Judging from annotated collections at Florence and Geneva, this is the plant Choisy called *Vismia rufescens*.

36. *Vismia glaziovii* Ruhl. Bot. Jahrb. Engler 30: Beibl. 67: 27. 1901.

"Frutex ramis teretiusculis vel paullum compresso-tetragonis, pruinoso-canescens, cito glabriusculis, internodiis 5–6 cm longis; foliorum petiolis circiter 1 cm longis, supra leviter canaliculatis, primum dense incano-puberulis, foliorum lamina ovata, basi rotundata, cuspidato-acuminata, apice ipso obtuso instructa, 10–15 cm longa, paullo infra medium 5–6 cm lata, integerrima subcoriaceo-

chartacea, supra pallide subolivaceo-vel glaucescenti-viridi, nitida, glaberrima, subtus tomento in junioribus uberiore, canescente, e pilis stellatis, hyalinis vel basi spadiceolis formato instructa, penninervi, venis ordinis primarii 12–16 parallelis, 7–14 mm distantibus, reticulatim anastomosantibus; thyrsis terminalibus et axillaribus, pedunculatis, 4–8 cm longis, rhachide, ramis, pedicellis dense incano-, rare subferrugineo-tomentosis; calycis laciniis oblongo-ellipticis vel lato-lanceolatis, extus densissime et persistenter incano-tomentosis, intus glabris et 3–5-vittatis, integerrimis, tenuiter membranaceo-marginatis, planis vel vix concavis; petalis flavescenscentibus calycem dimidio superantibus, evittatis et epunctatis, obovatis, brevissime unguiculatis, acutiusculis, flabellato-venosis, flavis (?), extus glabris, intus dense pilis incanis, rigidulis vestitis; staminibus multipartitis, villosis, calycem superantibus; staminodiis parvis, ellipticis, obtusiusculis, crassiusculis, praesertim apice longe villosis, vix 1 mm aequantibus; germine globoso, glabro, 2–2.5 mm longo; stylis 3 mm longis, filiformibus, rectis vel subflexuosis, capitellatis.”

SYNTYPES: “Brasilia: civit. Goyaz ad Corrego Fundo in sylvis prope Jaragua, m. Aug. fl. (*Glaziou* n. 20694), ibidem in sylvis ad Rio Areas, m. Sept. fl. (*Glaziou* n. 20695).” Photo FM 9162, of a specimen in the Berlin Herbarium, bears a printed label indicating it as *Glaziou* 20695, the second syntype cited, and a handwritten ticket reading “*Glaziou* 20694, Corrego Fundo dans le bois près de Jaragua, Goyaz, 23 Août 1895; arbuste; fl. jaunâtre,” indicating the first syntype. The plant is certainly authentic, but which syntype it is is uncertain.

I was first inclined to include the name as a synonym of *Vismia pentagyna* or, less satisfactorily, of *V. reichardtiana*. However, *V. glaziovii* comes from an area floristically different from Ceará and, on the basis of other instances of local Brazilian species studied in this and other genera, I am tentatively accepting the species pending more evidence. The leaves, judging from the type collection alone, are broadly ovate, more like those of *V. latifolia* than either *V. pentagyna* or *V. reichardtiana*, and the raceme is more densely crowded and the small flowers are more numerous. The pubescence of the lower leaf-surface agrees with that of *V. reichardtiana*.

37. *Vismia rusbyi* Ewan, sp. nov.

Planta fruticosa vel arborescens, intricate ramosa, dense foliosa, ramis superioribus tomentulosis, inferioribus glabrescentibus; laminis foliorum ovatis vel lanceolato-ovatis, 11–13 cm. longis, 5–6 cm. latis, submembranaceis, supra pallidis, venis subtus obscuris, subtus cano-pubescentibus, punctulatis, venulis secundariis anastomosantibus in venulam submarginalem; petiolis gracilibus, 10–15 mm. longis; paniculis cymosis, compactis, 4–5 cm. longis; calycibus brevibus, divaricatis, sepalis anguste ovatis, 5 mm. longis, sparse tomentulosis,

valde membranaceis secus margines, atro-vittatis; petalis valde exsertis, intus glanduloso-vittatis, extus venulis hirsutis, laminis rufo-tomentosis.

Shrub or small tree with shortly branching leafy branchlets, these finely tomentulose above, glabrescent below; leaf-blades ovate or lance-ovate, 11–13 cm. long, 5–6 cm. wide, rather thin-textured, dull above, the veins obscure, finely brownish or silvery pubescent beneath, glandular-punctulate, the secondary veins connecting in a submarginal vein; petioles slender, 10–15 mm. long; flowers crowded in a short cymose panicle 4–5 cm. long; calyces short, the sepals soon spreading, narrowly ovate, 5 mm. long, thinly tomentulose, the thin membranous border prominent, more or less black glandular-vittate; petals about 1.5 times as long as the calyx, vittate-glandular, the veinlets appressed-hairy beneath with simple hairs, heavily reddish tomentose; fruit unknown.

Type in the U. S. National Herbarium, no. 1,516,639, collected at San Carlos, Mapiri region, Bolivia, alt. 850 meters, flowers Dec. 16, 1926, fruit Feb. 21, 1927, by Otto Buchtien (no. 888); isotypes in the herbaria of the Royal Botanic Garden, Edinburgh, the Chicago Natural History Museum, the Missouri Botanical Garden, and the New York Botanical Garden.

PARATYPES:

PERU: SAN MARTÍN: Moyobamba, *Mathews* 1311 (OXF). HUÁNUCO: Cuchero, *Poeppig* 1361 p.p. (BM, F, OXF). PUNO: Santo Domingo, 1550 m., *McCarroll* 99 (NY); (?) 3 km. above Santo Domingo, 1950 m., *Metcalf* 30643 (US, cf. below).

BOLIVIA: Hacienda Casana, Tipuani Valley, 1400 m., *Buchtien* 7610 (US). Tipuani-Guanai, *Bang* 1695 (E, F, G, K, US, WU). Mapiri, 1500 m., *Rusby* 722 (BM, E, F, G, K, MO, P, US). Rurrenabaque, 300 m., *Rusby* 837 p.p. (K, NY, US), 1271 (NY, US). Sorata, *Bang* 1724 p.p. (F). Guanai, 600 m., *Rusby* 860 (NY). Lake Rogagua, 300 m., *Rusby* 1667 (NY, US).

Vismia rusbyi is related to *V. guianensis* and may be considered the southern Andean representative of that more northern species, from which it differs in having the petals prominently vittate with black glands. Furthermore, the leaves are finely pubescent and generally larger than those of *V. guianensis*; were it not for the glandular-punctulate lower surface, collections might be taken for the Bolivian *V. buchtienii*.

Though *Rusby* 722 is unquestionably *Vismia rusbyi* the specimens of that collection are variable among different herbaria; evidently specimens were collected from several trees in making up the sets. For this reason it has seemed preferable to select the more uniform series of *Buchtien* 888 as type.

Metcalf 30643 (US) from Peru may prove to be another, perhaps undescribed species. The leaves are oblong and notably thicker, and the petioles are longer and thicker, but more technical characters are wanting.

Tentatively placed here is another Peruvian collection, *Stork & Horton* 9582 (F, G, NA), from west and above Puente Durand, north of Huánuco, 1800 m., Department of Huánuco, Peru, which has the vestiture and floral characters of this species but deltoid-ovate, acute leaves that are unusually coriaceous for *V. rusbyi* and suggest *V. baccifera* subsp. *subcuneata*. It is described by the collectors as a "tree to 6 m., bark brown; wood hard." Evidently *Poeppig* 1361 from Cuchero, Peru, cited above, is the same form.

As indicated under *Vismia pentagyna*, there is a close affinity between that species of eastern Brazil and *V. rusbyi*, and both species seem to be extralimital segregates of the more northern typically glabrate *V. guianensis*.

38. *Vismia pentagyna* (Spreng.) Ewan, comb. nov.

Symplocos pentagyna Spreng. Syst. Veg. 3: 340. 1826.

Vismia decipiens Schlecht. & Cham. Linnaea 3: 116. 1828. Renaming of *Symplocos pentagyna* Spreng.

V. decipiens var. *laurifolia* Schlecht. & Cham. loc. cit. Based on *Symplocos pentagyna*.

V. decipiens var. *pyrifolia* Schlecht. & Cham. op. cit. 117. Type: Brazil, *Sellow*. Probable isotypes are *Sellow* 158, from "prov. Bahia inter Bahia et Victoria," (E, K, L, Photo FM 9161, of a specimen in the Berlin Herbarium; the latter photograph is labeled var. *pyrifolia* and may be part of the holotype).

Acrossanthes lhotzkyanus Presl, Bot. Bemerk. in Abhandl. Boehm. Gesell. Wiss. V, 3: 453. 1845. Type: Rio de Janeiro, Brazil, *Lhotzky* (not seen).

Caopia decipiens Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: Brazil, *Sellow*.

ADDITIONAL SPECIMENS EXAMINED:

SURINAM: Without locality, *Hostmann & Kappler* 1249 p.p. (F, FI, G, NY, P).

BRAZIL: RIO DE JANEIRO: *Glaziou* 10341 (K), 13571 (K). AMAZONAS: Manáus, *Schultes* 8086 (US), *Corner* 65 (NY); Parintins, January 16, 1936, *Ducke* 130 p.p. (US); Patua, Rio Negro, *Baldwin* 3270 (atypical, US), *Ule* 5963 (G); San Gabriel, *Spruce* 2170 p.p. (P). PARÁ: Belém, *Dahlgren & Sella* 355 (US), *Archer* 7712 (NY, US). PERNAMBUCO: Victoria, *Pickel* 3594 (US). BAHIA: Without locality, *Blanchet* 1862 (FI, OXF, P), *Glocker* 88 (G); Mount Toboa, Bomfim, *Curran* 156 (F, NY, UC, US).

Vismia pentagyna is related to *V. rusbyi* of the more interior districts of the Amazonian basin, and perhaps even more closely related to *V. reichardtiana* of eastern Brazil. *V. pentagyna* and *V. rusbyi* are contrasted in the key to the species. *V. reichardtiana* may be compared with *V. pentagyna* as follows:

	<i>pentagyna</i>	<i>reichardtiana</i>
Leaves	ovate to ovate-elliptic, attenuate at the base	lanceolate, rounded or acute at the base
Panicle	small, crowded, sessile	larger, loosely flowered, pedunculate
Petals	punctate, vittate, usually strongly so	not punctate, weakly vittate, if at all

The description of *Symplocos pentagyna* Spreng. is brief but adequate. It reads:

“pentagyna* 15. S [ymplocos] foliis oppositis oblongo-lanceolatis acuminatis integerrimis glabris, floribus racemosis 5-gynis. *Brasil.* Sello.”

The superscript asterisk indicates in the customary manner a species described as new. Chamisso and Schlechtendal recognized this Sellow collection as a *Vismia* and, according to a procedure then common in systematic botany, renamed it rather appropriately “*Vismia decipiens*.” There is no reason for abandoning Sprengel’s original epithet.

It is singular that when A. Brand monographed the Symplocaceae in Engler’s *Das Pflanzenreich* (1901) he did not dispose of Sprengel’s binomial in the section “Species excludendae,” nor mention the species in the account elsewhere. Evidently the inclusion of the binomial *Acrossanthes lhotskyanus* in the *Index Kewensis* was based on Reichardt’s citation of it since Presl’s obscure is name not listed elsewhere.

When describing *Vismia decipiens* Schlechtendal and Chamisso recognized two component varieties among Sellow’s material, differentiated on the basis of leaves, calyx segments, and petals. Of these distinctions the most obvious is the shorter-leaves of var. *pyrifolia* (leaves 9–10 cm. long) as contrasted with the longer-leaves of var. *laurifolia* (leaves 10–16 cm. long). Unfortunately, the number of sheets available of *V. pentagyna* are too limited to warrant conclusions on these varieties.

Reichardt placed *Vismia decipiens* near *V. confertiflora* in his treatment of the Brazilian species, but I do not believe its relationship with that species is very close. Both *Vismia pentagyna* (i.e. *V. decipiens* of former accounts) and *V. reichardtiana* are more closely related to *Vismia guianensis* than to *V. confertiflora*, when one disregards the pubescence character unduly stressed by Reichardt in his groupings “Rufescentes” and “Dealbatae.” The very youngest leaves of *Vismia pentagyna* may be rufous-tomentose beneath (e.g. *Curran* 156 (F) from Bomfim, Bahía), but the pubescence is early deciduous and the mature leaves are glabrescent with a very fine close, at times grayish, puberulence.

39. *Vismia buchtienii* Ewan, sp. nov.

Arbor nana vel suffrutex 5–9 m. altus, ramis gracilibus, paullo compressis, glabrescentibus, apicibus rufo-pubescentibus; laminis foliorum lanceolato-ovatis, acuminatis, 9–15 cm. longis, 3.5–5.5 cm. latis, supra lucidis, infra opacis, argenteo-pubescentibus vel minute stellato-lepidotis, costa prominente, venis secundariis manifestis, petiolatis, petiolis longis (12–16 mm.); paniculis ramosis, ramis divaricatis et patentibus, interdum inflorescentiis adjunctis in axillis

foliorum supremorum, omnibus rachibus et ramis rufo-tomentellis; sepalis brevibus, anguste ovatis, vix acutis, cinereo-tomentellis, 4.5–5.0 mm. longis, sepalis alternis anguste marginatis, marginibus membranaceis vittatis et minute ciliolatis; petalis ovatis, quam sepalis duplo longioribus, minute lineatis, intus dense tomentosis; staminibus inclusis; fructibus oblongis vel ovoideis, 6–12 mm. longis.

Low tree or shrub 5–9 m. high, with slender branchlets, these a little flattened, glabrescent in age, finely rufous-pubescent at the tips; leaves lance-ovate, acuminate, 9–15 cm. long, 3.5–5.5 cm. wide, shining above, dull, more or less silvery pubescent or lepidote beneath with scattered fine stellate hairs, especially along the midrib, the secondary veins evident, moderately long-petiolate, the petioles 12–16 mm. long; flowers in a short, loosely divaricate panicle with at times supplementary floriferous branchlets in the uppermost leaf-axils, the rachis and branchlets rufous-tomentulose; calyx short, cinereous-tomentulose, the tomentum in low longitudinal ribs, the sepals narrowly ovate, barely acute, 4.5–5.0 mm. long, the alternate sepals with narrow dark-vittate membranous margins, finely ciliate; petals ovate, about twice as long as the sepals, finely lineate, densely tomentose within; stamens included; fruit oblong or ovoid, blackish 6–12 mm. long.

Type in the U.S. National Herbarium, no. 1,159,313 collected at San Antonio, Mapiri region, Bolivia, alt. 850 meters, in December 1907, by Otto Buchtien (no. 2022); isotype in the Rijksherbarium, Leiden.

PARATYPES:

PERU: SAN MARTÍN: Moyobamba, 800–900 m., *Weberbauer* 4520 (G), in 1838, *Mathews* (FI, K); Corico, 1500–1800 m., Dec. 1865, *Pearce* (K); Tarapoto, 750 m., *L. Williams* 5954 (F); Lamas, 840 m., *L. Williams* 6344 (F).

BOLIVIA: LA PAZ: Basin of Río Bopi, San Bartolomé, near Calisaya, 750–900 m., *Krukoff* 10215 p.p. (G, K, MO, NY, US); San Carlos, Mapiri region, 850 m., *Buchtien* 886, (US), 887 (US); Copacabana, about 10 km. south of Mapiri, Prov. Larecaja, 850–950 m., *Krukoff* 11042 (F, G, K, S, US); Unduavi, 2400 m. *Rusby* 719 (NY). SANTA CRUZ: Buena Vista, Province of Sara, *Steinbach* 6527 (BM, E, F, K, MO, NY, S, U, UC).

BRAZIL: MATO GROSSO: *Moore* 137 (BM), 609 (BM, E, NY, WU); Santa Anna da Chapada, *Malme* 2076 (S, one sheet of leaves pinked by leaf cutting ants!); Burity, northeast of Cuyabá, 675 m. *Collenette* 167 (K, NY).

Vismia buchtienii is most closely related to *V. rusbyi*, which it resembles in its leaf characters, but that species has shorter, more broadly ovate leaf-blades, which are finely punctate beneath. The pubescence of the lower leaf-surfaces is very similar; however, *V. rusbyi* is finely pubescent with short curling but unbranched hairs. The sepals are more densely tomentose in *V. buchtienii*. In *V. rusbyi* the secondary veins anastomose in a submarginal loop, whereas in *V. buchtienii* they are free to the margin.

40. *Vismia amazonica* Ewan, sp. nov.

Arbor 3–15 m. alta, trunco gracili, 3–5 cm. diam., ramis castaneis, deorsum glabris, sursum aliquantum rufo-tomentulosis sicut axibus panicularum; foliis superioribus non reductis, laminis omnibus ovatis, basi obtusis, apice acuminatis, cuspidatis, vel saepe subcaudatis, supra glabris et nitentibus, subtus subglabratiss, valde sparse rufo-tomentellis praecipue in venis secundariis, 12–15 cm. longis, 5.5–8.0 cm. latis, petiolatis, petiolis gracilibus 12–14 mm. longis; paniculis dense cymiformibus 8–10 (13) cm. longis, pedicellis ultimis ca. 5 mm. longis; floribus parvis; sepalis 5 (6) mm. longis, dense tomentellis, marginibus membranaceis et angustis 0.5 mm. latis, ciliolatis vel subciliatis; petalis obovatis ovalibusve, breviter unguiculatis, 5–8 mm. longis, simpliciter lineatis, intus villosissimis viridi-flavis; staminibus inclusis; fructibus ignotis.

Tree 3–15 m. high, the trunk slender, 3–5 cm. in diameter breast high, the branchlets chestnut-brown and more or less rufous-tomentulose, like the rachis of the inflorescence; leaves little if at all reduced up to the panicle, the blades all ovate, rounded at the base, acuminate or cuspidate or often contracted to a slender subcaudate tip, glabrous and shining above, appearing glabrous below, but actually thinly rufous-tomentulose beneath, more strongly so along the larger veins, 12–15 cm. long, 5.5–8.0 cm. wide, the petioles slender, 12–14 mm. long; panicle compactly cymosely branching, 8–10 or 13 cm. long, the ultimate pedicels about 5 mm. long; flowers small, the sepals mostly 5 (rarely 6) mm. long, closely tomentulose with a narrow membranous border about 0.5 mm. wide, ciliolate along the whole margin or at least on the distal half; petals obovate or oval, short-clawed, 5–8 mm. long, simply lineate with fine dark lines, copiously hairy within, greenish-yellow, the unopened buds light gray-green; stamens included; fruit unknown.

Type in the U.S. National Herbarium, no. 1,461,142, collected at Iquitos, Department of Loreto, Peru, alt. about 100 meters, Aug. 2–8, 1929, by E. P. Killip and A. C. Smith (no. 27378).

PARATYPES:

BRITISH GUIANA: Karinyi, Upper Essequibo River, *Myers* 5764 (K, panicle exceptionally open).

COLOMBIA: CAQUETÁ: Sucre, banks of Río Hacha, 1000 m., *Cuatrecasas* 9015 (US).

PERU: LORETO: Mishuyacu, near Iquitos, 100 m., *Klug* 317 (F, US), "pichirina," *Klug* 1524 (US). **SAN MARTÍN:** Tarapoto, 750 m., *L. Williams* 5379 (F, US); Moyobamba, *Sandeman* 163 (K, OXF).

BOLIVIA: COCHABAMBA: Colonia Presidente Busch, Puerto Polonia, Río Coni, 14 km. east of San Antonio, 395 m., *Cárdenas & Cutler* 7202 (US).

BRAZIL: AMAZONAS: Parintins, *Ducke* 130 p.p. (A, F); near Urucurituba, Munic. Borba, *Krukoff* 5946 (BM, G, K, S, U, US). **PARÁ:** Upper Rio Cupary,

plateau between Xingu and Tapajos Rivers, *Krukoff* 1075 (A, BM, G, K, S, U), 1175 (A, BM, G, K, S, U); Belém, Utinga, *Schultes* 8071 (US); Santarem, May 1850, *Spruce* (CGE, NY, TCD).

Most of the collections of *Vismia amazonica* have been identified previously as *V. confertiflora*. *V. amazonica* was distinguished from that species, however, by Eyma, in the Utrecht Herbarium without proposing a name for it. Its small flowers recall *V. micrantha*, although actually they are somewhat larger and intermediate in size between the *V. micrantha* group and the Section *Euvismia*. The leaves of *V. amazonica* average definitely smaller than those of *V. confertiflora* and are ovate and acuminate rather than ovate-oblong and obtuse. *V. amazonica* may be distinguished from *V. reichardtiana* of eastern Brazil, which it recalls in its lustrous shining leaves, by the ovate rather than lanceolate blades. *V. amazonica* differs from *V. confertiflora* in that the sepals of the former have the hyaline border distinctly ciliolate. The upper surface of the leaf-blades in *V. amazonica* is yellowish-green and shining, and the leaf-blades are smaller and often rhomboid, whereas in *V. confertiflora* they are generally larger and ovate.

41. *Vismia confertiflora* Spruce ex Reich. in Mart. Fl. Bras. 12¹: 205. 1878.

Caopia confertiflora Kuntze, Rev. Gen. Pl. 1: 59. 1891.

? *V. gracilis* Hieron. Bot. Jahrb. Engler 20. Beibl. 49: 52. 1895. TYPE: Zamora, "East Andes of Loja," Ecuador, 500–1200 m., *Lehmann* 7735.

The locality determined by reference to Lehmann's ms. field notes in the U.S. National Herbarium. (Isotype, K).

? *Caopia gracilis* Kuntze, loc. cit.

TYPE: Vicinity of Santarem, Pará, Brazil, September 1850, *Spruce* 1087 (isotypes BM, CGE, E, FI, G, K, NY, OXF, TCD, W).

ADDITIONAL SPECIMENS EXAMINED:

COLOMBIA: META: Sabanas de San Juan de Arama, Río Güejar, 500 m., *Idrobo* & *Schultes* 1199 (US). VAUPES: Río Piraparaná, *Schultes* & *Cabrera* 17321 (NO, US), 17363 (US). AMAZONAS-VAUPÉS: Raudal Yayacopi, 240 m., *Schultes* & *Cabrera* 15365 (US); Raudal Jirijirimo, 270 m., *Schultes* & *Cabrera* 14978 (US); Jinogojé, 210 m., *Schultes* & *Cabrera* 19830 (US). AMAZONAS: Loretoyacu River, Trapecio Amazonico, 100 m., *Schultes* 6668 (US), *Schultes* & *Black* 8542 (US); Caño Guacayá, Río Miritiparaná, *Schultes* & *Cabrera* 16272 (NO, US). PUTUMAYO: Mocoa, *Sprague* 361 (BM, K), *Schultes* & *Cabrera* 19070 (US); Río Putumayo, Puerto Porvenir, near Puerto Ospina, 250 m., *Schultes* 3401A (US), *Schultes* & *Cabrera* 18986 (US); Umbría, 325 m., "pichirina," *Klug* 1861 (A, F, K, S, US).

ECUADOR: EL ORO: Along quebrada on south and west slopes of Montaña Sichicay, near Cachicarán, on a tributary of Río Minas Nuevas, above Huertas, east and northeast of Paccha, 2135–2285 m., "jerigoa," "leaves buff-brown below; calyx ferruginous-brown without, pale green within; petals green without, white-hairy within; ovary orange; bark brownish-ruddy, peeling like sycamore or Myrtaceae, inside of bark orange, staining orange and with gummy resin; wood white, inferior," *Steyermark* 54112 (US) [cf. *V. gracilis* Hieron.]. LOJA: *André* 4600 (K). NAPO-PASTAZA: Zatzayacu, 400–500 m., *Mexía* 7084 (NA, UC, US),

7113 (F, NA, NY, UC, US); Puyo, *Sydow* 876 (US). SANTIAGO-ZAMORA: Along Quebrada Achupallas, 3000–3500 m., *Steyermarck* 54530 (US) [cf. *V. gracilis* Hieron.].

BRAZIL: AMAZONAS: Santarem, *Spruce* 766 p.p. (P); Tabatinga, *Ducke* 1883 (K, US).

The sepals of *Vismia confertiflora* have a broad hyaline flange contrasting sharply with the body of the sepal. The leaves have a silvery, almost lepidote appearance from the very thin puberulence, distinguishing it from *V. obtusa*, of the same region, which is wholly glabrous, and punctate beneath with scattered raised black dots. Both species may have at times short-acuminate leaf-tips.

Vismia confertiflora is a tree of dense bushy habit about 10 to 15 meters high, with gummy orange-red juice, and yellow petals. The fruit is evidently green when ripe, to judge from the collectors' field-notes. *V. tomentosa*, another species of the upper Amazon basin, agrees with *V. confertiflora* in its narrowly obovate, finely vittate, yellow petals, but the pubescence of the sepals in *V. tomentosa* is truly a tomentum, being denser, more felt-like, than the close fine puberulence of *V. confertiflora*. Both have the floral leaves exceeding the panicles, long-petiolate, broadly ovate principal leaves, prominent flanges on the evittate sepals in flower, and strongly spreading to reflexed sepals in fruit. The fruit in *V. confertiflora*, however, is green at maturity and in *V. tomentosa* dark brown. There is some evidence that the habitats contrast to some degree, *V. confertiflora* being a spreading tree of the dense upland forests and *V. tomentosa* a taller, more ponderous species of the lowland "high forests." The collections studied of *V. confertiflora* from British Guiana show smaller leaves and not so prominent hyaline margins of the sepals. In British Guiana the species is a shrub or small tree about four meters high. *V. gracilis*, of Ecuador, represents a narrow-leaved phase which may prove distinct when better known.

42. *Vismia obtusa* Spruce ex Reich. in Mart. Fl. Bras. 12¹: 207. 1878.

Caopia obtusa Kuntze, Rev. Gen. Pl. 1: 59. 1891.

TYPE: "Rio Negro, gapó, Feb. 1851, slender tree 25 ft.," vicinity of Manáus, Brazil, *Spruce* 1352 (Photo FM 19550, of specimen in Munich Herbarium; isotypes, K, P).

ADDITIONAL SPECIMENS EXAMINED:

COLOMBIA: HUILA: Río Suaza, 1650 m., *Little* 8540 (NA, atypical). AMAZONAS: Río Hamacayacu, Trapecio Amazónico, between Amazon and Putumayo watersheds, 100 m., *Schultes* 8242 (US).

ECUADOR: PICHINCHA: Mindó, *Sydow* 297 (US); Santo Domingo de Colorado, *Little* 6171 (F, US). NAPO-PASTAZA: Tena, 400 m., *Mexía* 7153 (US, NA, UC), 7167 (UC, US). ESMERALDAS: San Lorenzo, *Little* 6330 (F, US).

PERU: LORETO: Gamitanacocha, Río Mazán, 100–125 m., *Schunke* 264 (A, F, NA, UC, US).

BRAZIL: AMAZONAS: Banks of Igarapé do Crespo, above Cachoeirinha, near Manáus, "lacre," *Ducke* 697 (US).

Vismia obtusa occasionally bears axillary panicles, supplementary to the usual terminal inflorescence, as in the type collection, or in lieu of it, as in *Mexia* 7153. When the panicles are axillary rather than terminal the species suggests *V. lateriflora* Ducke, which has the leaves more or less cordate at the base and tomentose beneath. Ynes Mexia described this species as a spreading shrub with white flowers (label of *Mexia* 7153).

Spruce (or Benthham?) may have divided the original collection into two portions: the February, 1851, "Manáus" collection, and a second, Dec.-Feb. 1850-51, "Barra" collection (CGE, E, F, G, OXF, TCD, W) sometimes numbered "1352," which is a very close match for the Manáus type.

43. *Vismia sprucei* Sprague, Trans. Bot. Soc. (Edinburgh) 22: 428. 1905.

TYPE: Vicinity of Panuré, Rio Vaupés, Brazil, *Spruce* 2601 (K). (Isotypes, BM, C, F, G, NY, OXF, TCD, W).

ADDITIONAL SPECIMENS EXAMINED:

COLOMBIA: VAUPÉS: Guaracapuri Cachoeira, east of Mitú, Río Vaupes, *Allen* 3375 (US).

ECUADOR: NAPO-PASTAZA: Río Pastaza, between Río Topo, at Topo, and Mera, 1158-1675 m., *Steyermarck* 54899 (F, inflorescences both axillary and lateral, US).

PERU: LORETO: Yurimaguas, Lower Río Huallaga, 135-180 m., *Poeppig* 2411 (W), *Killip & Smith* 27541 (F, US), *Mexia* 6078 (BM, CAS, F, G, K, NO, NY, S, U, UC, US); Caballo-Cocha, *L. Williams* 2074 (F); La Victoria, *L. Williams* 3014 (F, US); Mishuyacu, 100 m., *Klug* 745 (US). HUÁNUCO: Huacachi, near Muña, *Macbride* 4089 (F); Lower Río Huallaga, *L. Williams* 3827 (F); Huallaga, 1500-1600 m., *Weberbauer* 6803 (F, US), ca. 1200 m., *Macbride* 4229 (F); Chinchao, *Sawada* 84 (F); Middle Río Ucayali, "pichirina," *Tessmann* 3278 (F, NY, Photo FM 9167, of specimen in Berlin Herbarium bearing manuscript name meaning oval-leaved).

BRAZIL: AMAZONAS: Matupiry, basin of Rio Jurua, *Krukoff* 4597 (UC, US); Borba, Rio Madeira, August 1828, *Riedel* 1318 (US); Cobija, Rio Acre, *Ule* 9614 (G, K, L).

Vismia sprucei is well marked by the shining amphiglabrous leaves with areolate veins. *V. obtusa* shares the same crowded habit of its foliage, especially below the inflorescence, but in that species the blades are rounded or barely acute not apiculate, the upper leaf surface is dull, the petioles are generally longer, and the texture thinner. The sepals even in bud are glabrous; in *V. obtusa*, they are tomentose, the tomentum thinning in age. *V. sprucei* varies in leaf shape from oval, the usual typical condition, to lanceolate. Like *V. obtusa*, it is constant in having the leaves punctate, with marginal vein-loops.

On the trail to San Ramón, near Yurimaguas, Loreto, Peru, Mrs. Mexia noted this species (her no. 6078) as a "shrub 3 m. high, many

branched; white flowers; juice orange-colored, staining. Abundant." She recorded the vernacular name as "pichirina."

During my early studies of the genus I thought *Vismia sprucei* undescribed, overlooking Sprague's description and the isotype preserved in the New York Botanical Garden, and named the presumed new species for Ynes Mexía (1870–1938). Collections encountered that are so annotated should be referred to this species.

Uncertain Species or Names

Hypericum lanceolatum Lam. ex Steud. Nom. Bot., ed. 1, 420. 1821. *Nom. nud.*

No specimen so labeled was found in the Lamarck Herbarium at Paris.

Hypericum petiolatum L. Sp. Pl., ed. 3, 1102. 1764.

Caopia petiolata Kuntze, Rev. Gen. Pl. 1: 59. 1891.

Not identifiable. There is no specimen so labeled in the Linnaean Herbarium, London. The original description is as follows:

"*Hypericum floribus trigynis, foliis ovatis petiolatis integerrimis subtus tomentosis, caule fruticoso tetragono compresso.*

"*Habitat in Brasilia.*

"*Statura & Stamina H. Lasianthi. Caulis tetragonus, obtusus. Stipulae nullae. Folia Citri, petiolata, acuta, subtus obsolete tomentosa. Corymbus brachiatus. Stamina phalanges oblongae, maxime spectabiles.*"

Vismia guianensis* var. β *glabrata Choisy in DC. Prodr. 1: 542. 1824.

Based on *Hypericum bacciferum* Marcgr. bras. 96. *fig. 1.*, a Brazilian plant, and, in part, on a drawing of a Mexican plant identified by the citation "Moc. et Sesse, Ic. fl. Mex. ined."

A supporting collection has not been located in the de Candolle Herbarium.

Vismia humboldtiana Schlecht. & Cham. Linnaea 3: 118. 1828.

Vismia latifolia H.B.K. Nov. Gen. & Sp. 5: 183. 1822; non *V. latifolia* (Aubl.) Choisy (1821).

TYPE: Banks of Río Cassiquiare, Amazonas, Venezuela, *Humboldt & Bonpland* (presumably at P).

Vismia humboldtiana Schl. & Cham. is a renaming of *V. latifolia* H.B.K., non *V. latifolia* Choisy, which is based on *Hypericum latifolium* Aublet. The type has not been studied. The original description is as follows:

"*V. ramulis subpuberulis; foliis ovato-ellipticis, acuminatis, subcordatis, supra nitidis, subtus calycibus tenuissime ferrugineo-tomentosis; paniculis terminalibus, simplicibus, pedunculatis.*

"Crescit ad ripam fluminis Cassiquiare. Floret Aprili.

"Arbor ramulis compresso-tetragonis, laevibus, glabris, junioribus tenuissime puberulis. Folia opposita, petiolata, ovato-elliptica, acuminata, basi rotundata, subcordata, integerrima, reticulato-venosa, nervo medio venisque primariis subtus prominentibus, subcoriacea, supra glabra, viridia et nitida, subtus punctulata et tenuissime ferrugineo-tomentosa, pilis stellatis, 4-4½ pollices longa, 2-2½ pollices lata. Petioli semipollicares, tenuissime fuscescenti-tomentosi. Paniculae terminales, pedunculatae, solitariae, simplices, breves; pedunculo, pedicellis, rhachi ramisque angulatis, tenuissime ferrugineo-tomentosis. Flores pedicellati; in specimine nostro nondum aperti; pedicellis 2 lineas longis. Calyx quinquepartitus, externe tenuissime fusco-tomentosus; foliolis ovato-oblongis, acutiusculis, coriaceis, margine membranaceo-diaphanis, subaequalibus. Petala 5, subrotundo-obovata, externe glabra, interne villosa. Stamina Vismiae, in quinque phalanges coalita. Ovarium ovatum, glabrum. Styli 5 (?). Fructus desideratur."

Vismia jelskii Szyszyłowicz, Rozprawy, Akademia Umiejętności w Krakowie, Wydział Matematyczno-przyrodniczy, II, 9: 225. 1895.

The original description, taken from a copy in the National Library of Medicine, Washington, D.C., is as follows:

"Arborescens. Folia petiolata, petiolis dense nigro punctatis 2-3 cm. longis, laminibus ovato-ellipticis, basi rotundatis vel attenuatis, 12-17 cm. longis, 6-10 cm. latis, integerrimis, coriaceis, supra viridibus, glabris, subtus pruinoso-canescens glandulisque prominentibus nigro punctatis. Gemmae axillares stipitatae, glaberrimae. Thyrsi terminales 4-7 cm. longe pedunculati, prostrati, 8 cm. longi, 8-10 cm. lati, ramis patentibus glabris. Pedicelli 10-20 mm. longi, media parte articulati bracteolatique. Calyx intus glaber, extrinsecus pruinoso canescens, laciniis lanceolatis, 7-8 mm. longis, coriaceis, margine integerrimo anguste membranaceis, albo pubescentibus. Petala calyce subduplo longiora, oblongo spathulata, extrinsecus glabra, intus dense ferrugineo villosa. Staminodia claviformia, apicem versus pilosa. Staminum phalanges quinque, 8 mm. longae, multiandrae, filamentis specialibus, capillaceis, denso ferrugineo villosis. Ovarium ovoideum, glabrum, styli quinque, erecto-patentes, stigmatibus depresso-capitatis. Fructus (immaturus ?) baccatus, oblongus, 15 mm. longus, 10 mm. latus, glaber, calyce reflexo basi cinctus.

"*Vismiae dealbatae* H. B. K. et *Vismiae confertiflorae* Spr. proxima.

"Cutervo, Jelski no. 253."

Szyszyłowicz indicates (op. cit. 216) that Cutervo is in the Department of Cajamarca. The species is not definitely identifiable from the

description; it may be allied with *V. rusbyi*, since the description suggests very much the specimen *Metcalf* 30643, mentioned above under *V. rusbyi*. Szyszyłowicz work was perhaps issued as a doctoral dissertation under Zahlbruckner.

Vismia latifolia* var. *glabrescens Sagot, Ann. Sci. Nat. VI, 11: 163. 1881.

TYPE: An undesignated specimen in the de Candolle Herbarium, Geneva, "sub nomine *V. reticulata* Poiret."

This may represent *V. macrophylla* H. B. K.

Vismia laxiflora Reich. in Mart. Fl. Bras. 12¹: 203. 1878.

Caopia laxiflora Kuntze, Rev. Gen. Fl. 1: 59. 1891.

TYPE: Roraima, British Guiana [actually probably Venezuela], in 1841, *R. Schomburgk* 835 [an error for 837] (Isotypes: BM, F, FI, G, K, P, W, Photo FM 32271 of a specimen in the Vienna Herbarium). The type collection represents an immature, few-flowered plant of almost vinelike habit, unique among hundreds of collections examined. The corollas are unknown, but the calyx in bud and the characters of the leaves agree with *V. falcata* Rusby. No other *Vismia* has been collected on or near Roraima, unless a collection of *V. falcata* so labelled was in fact taken there [*Schomburgk* 935 (CGE)] and a collection of *V. sessilifolia* (*Schomburgk* 917).

Vismia schomburgkiana Klotzsch ex Schomburgk, Reisen in Brit.-Guiana 3: 999. 1848, *nom. nud.*

"Am oberen Pomeroon auf lichten Waldstellen. Blüht im September und October. Strauch," without a reference to a Schomburgk collection number.

Vismia sieberiana Klotzsch ex Schomburgk, loc. cit., *nom. nud.*

Based on an undesignated Schomburgk collection, identified by the same phrase as the preceding.

Numbered Specimens Cited

- ALLARD, H. A.
21629 *baccifera* subsp. *subcuneata*
- ALLEN, P. H.
1692 *viridiflora*
3375 *sprucei*
- ANDERSON, C. W.
40 *macrophylla*
- ANDRÉ, E.
1411 *baccifera* subsp. *ferruginea*
4600 *confertiflora*
- APPUN, C. F.
277 *japurensis*
- ARAQUE-MOLINA, J., and BARKLEY, F. A.
18S215 *baccifera* subsp. *dealbata*
19Ch047 *baccifera* subsp. *ferruginea*
19Ch134 *angusta*
- ARAQUE-MOLINA, N., et al.
350 *guianensis*
- ARCHER, W. A.
313a *laevis*
1323 *laevis*
1741 *baccifera* subsp. *ferruginea*
2304 *cayennensis*
2660 *cayennensis*
2706 *cayennensis*
7712 *pentagyna*
8053 *japurensis*
8243 *japurensis*
- BAILEY, L. H., and BAILEY, E. Z.
1335 *cayennensis*
- BAKER, C. F.
172 *reichardtiana*
- BALDWIN, J. T.
3270 *pentagyna*
- BANG, M.
595 *plicatifolia*
621 *plicatifolia*
683 *crassa*
- 835 *plicatifolia*
1695 *rusbyi*
1724 *p.p. baccifera* subsp. *subcuneata*, *p.p. rusbyi*
2931 *crasea*
2933 *plicatifolia*
- BARKLEY, F. A., et al.
113 *guianensis*
387 *guianensis*
- BARRETO, M.
1274 *micrantha*
2908 *brasiliensis*
2909 *brasiliensis*
2910 *micrantha*
2912 *micrantha*
4013 *martiana*
4035 *brasiliensis*
- BECCARI, N.
16 *japurensis*
- BILLBERG, J. I.
231 *billbergiana*
- BLACK, G. A.
2421 *guianensis*
47-937 *martiana*
24-2421 *guianensis*
- BLANCHET, J.
595 *reichardtiana*
1862 *pentagyna*
1933 *angusta*
3041 *reichardtiana*
3520 *reichardtiana*
- BONDAR, G.
3017 *reichardtiana*
- BRITTON, N. L., et al.
307 *guianensis*
724 *cayennensis*
821 *guianensis*
824 *cayennensis*
837 *falcata*
1336 *guianensis*
1778 *cayennensis*
2542 *cayennensis*

BROADWAY, W. E.

- 399 cayennensis
 555 guianensis
 3035 cayennensis
 4139 falcata
 4140 cayennensis
 5291 falcata?
 5661 falcata?
 5726 falcata
 6208 guianensis
 6837 guianensis

BUCHTIEN, O.

- 222 plicatifolia
 364 crassa
 886 buchtienii
 887 buchtienii
 888 rusbyi
 889 baccifera subsp. subcuneata
 890 baccifera subsp. subcuneata
 890a baccifera subsp. subcuneata
 1907 baccifera subsp. subcuneata
 2022 buchtienii
 2114 baccifera subsp. subcuneata
 4645 plicatifolia
 5464 plicatifolia
 6014 plicatifolia
 7610 rusbyi

BURCHELL, W. J.

- 10042 japurensis
 B[OSCH] W[ESSEN] (Surinam)
 459 latifolia
 635 cayennensis
 672 sessilifolia
 1404 latifolia
 1564 latifolia
 1676 latifolia
 1772 cayennensis
 2711 angusta
 2732 latifolia
 2869 latifolia
 2919 angusta
 4362 angusta
 4543 angusta

CÁRDENAS, M.

- 1947 plicatifolia
 4172 plicatifolia

CÁRDENAS, M., and CUTLER, H.

- 7202 amazonica

CARDONA, F.

- 386 japurensis
 1229 angusta
 1418 macrophylla
 2113 guianensis
 2200 guianensis
 2244 guianensis

CASARETTO, J. (GIOVANNI)

- 3510 micrantha

CHARDON, C. E.

- 137 baccifera subsp. ferruginea

CLAUSEN, P.

- 3 brasiliensis
 4 brasiliensis
 5 parviflora?
 27 magnoliifolia
 134 brasiliensis

COLLENETTE, C. L. ("ST. GEORGE
EXPEDITION")

- 167 buchtienii
 588 angusta (forma)

CORE, E. L.

- 620 laevis
 1519 sessilifolia

CORNER, A.

- 63 macrophylla
 65 pentagyna

CUATRECASAS, J.

- 3593 baccifera subsp. dealbata
 4568 baccifera subsp. dealbata
 4757 lauriformis
 4772 angusta
 7658 minutiflora
 8242 baccifera subsp. dealbata
 8605 cavanillesiana
 8819 guianensis
 9015 amazonica
 9047 japurensis
 9632 baccifera subsp. dealbata
 11305 angusta
 11385 tomentosa
 12932 baccifera
 13228 lauriformis
 13591 baccifera
 13954 cuatrecasasii

- 14081 panamensis
 14893 lehmannii
 15678 mandurr
 16049 cuatrecasasii
 16068 panamensis
 16354 panamensis
 16614 rufa
 16687 cuatrecasasii
 16903 macrophylla
 17120 panamensis
 17199 cuatrecasasii
 17449 rufa
 17551 panamensis
 17641 cuatrecasasii
 17694 cuatrecasasii
 18327 baccifera subsp. ferruginea
 18331 baccifera subsp. ferruginea
 19373 mandurr
 19738 panamensis
 21102 rufa
 21279 angusta
 21389 panamensis
 22276 tomentosa?
 23561 mandurr
 23868 baccifera
- CUATRECASAS, J., and GARCIA-BARRIGA, H.
- 10177 baccifera subsp. dealbata
- CUATRECASAS, J., and JARAMILLO, R.
- 11991 baccifera subsp. dealbata
- CUATRECASAS, J., and PÉREZ-ARBELÁEZ, E.
- 6750 macrophylla
- CURRAN, H. M.
- 67 cayennensis
 107 reichardtiana
 156 pentagyna
 183 baccifera subsp. ferruginea
- CURRAN, H. M. and HAMAN, M.
- 1010 baccifera subsp. dealbata
 1011 macrophylla
- DAMAZIO, L.
- 1328 micrantha
 1358 magnoliifolia
- DAHLGREN, B. E.
- 965 reichardtiana
- DAHLGREN, B. E., and SELLA, E.
- 355 pentagyna
- DANIEL, BROTHER
- 2197 laevis
 3850 baccifera subsp. ferruginea
 3852 laevis
 4101 mandurr
- DAWE, M. T.
- 871 macrophylla
- DE LA CRUZ, J. S.
- 1213 guianensis
 1446 p.p. macrophylla, p.p. sessilifolia.
 1744 macrophylla
 1853 angusta
 2011 guianensis
 2115 macrophylla
 2383 macrophylla
 2614 macrophylla
 2705 guianensis
 2760 guianensis
 2819 falcata
 2820 guianensis
 3149 japurensis
 3170 japurensis
 3255 macrophylla
 3382 macrophylla
 3730 sessilifolia
 3841 macrophylla
 3896 guianensis
 4175 guianensis
 4281 guianensis
 4321 guianensis
 4471 guianensis
- DELGADO, E.
- 132 baccifera subsp. ferruginea
- DOMBEY, J.
- 639 glabra
 640 glabra
- DUCKE, A.
- 117 cayennensis
 130 p.p. amazonica, p.p. pentagyna
 206 tomentosa
 392 macrophylla
 697 obtusa
 930 cauliflora

- 1068 *macrophylla*
 1882 *cayennensis*
 1883 *confertiflora*
 12494 *sessilifolia*
 21274 *reichardtiana*
 25054 *lateriflora*
 25055 *cauliflora*
- DUGAND, A.
- 3688 *baccifera* subsp. *dealbata*
- DUGAND, A., and JARAMILLO, R.
- 2917 *angusta*
 3977 *baccifera* subsp. *dealbata*
- EGGERS, H. F. A.
- 1078 *guianensis*
 1118 *falcata*
 1363 *cayennensis*
 1380 *guianensis*
 1411 *guianensis*
 1420 *falcata*
 5731 *cayennensis*
 13031 *baccifera* subsp. *dealbata*
- EWAN, J. A.
- 15860 *baccifera* subsp. *ferruginea*
- FANSHAWE, D. B.
- F627 *macrophylla*
- FENDLER, A.
- 6 *viridiflora*
 8 *macrophylla*
 41 *lindeniana*
 299 *viridiflora*
- FOCKE, H. C.
- 382 *angusta*
- FORESTRY DEPARTMENT B[BRITISH]
 G[GUIANA]
- 3726 *sandwithii*
 3805 *sandwithii*
 6469 *angusta*
 6480 *sandwithii*
- FOSBERG, F. R.
- 19851 *baccifera* subsp. *ferruginea*
 20173 *baccifera* subsp. *dealbata*
 21604 *baccifera* subsp. *ferruginea*
- FOSBERG, F. R., and GRANT, M. L.
- 21966 *baccifera* subsp. *dealbata*
- FROES, R. L.
- 22948 *cayennensis*
- FUNCK, N., and SCHLIM, L.
- 101 *lindeniana*
- GARCIA-BARRIGA, H.
- 8377 *angusta*
 10989 *baccifera* subsp. *dealbata*
 11778 *lauriformis*
 12261 *laevis*
 13784 *tomentosa*
- GARDNER, G.
- 321 *magnoliifolia*
 329 *magnoliifolia*
 939 *reichardtiana*
 946 *reichardtiana*
 2491 *reichardtiana*
- GAY, C.
- 939 *minutiflora*
- GEHRIGER, W.
- 351 *baccifera* subsp. *dealbata*
- GILLESPIE, J. W.
- P12 *panamensis*
- GLAZIOU, A. F. M.
- 2946 *magnoliifolia*
 10341 *pentagyna*
 11804 *magnoliifolia*
 12465 *martiana*
 13571 *pentagyna*
 20694 *glaziovii*
 20695 *glaziovii*
- GLEASON, H. A.
- 64 *sessilifolia*
 340 *macrophylla*
 345 *guianensis*
 480 *macrophylla*
 481 *falcata*
 551 *macrophylla*
 709 *guianensis*
- GLOCKER, C.
- 88 *pentagyna*

GRAHAM, E. H.

- 147 guianensis
292 sessilifolia

GRANT, M. L., and DREW, W. B.

- 10653 mandurr

GUILLEMIN, J. B. A.

- 498 brasiliensis

GUTIERREZ, G., and BARKLEY, F. A.

- 17C679 baccifera subsp. baccifera
17C680 baccifera subsp. ferruginea

GUTIERREZ, G., ET AL.

- 125 guianensis
931 japurensis

HAUGHT, O.

- 4885 angusta

HAYES, S.

- 456 viridiflora
921 panamensis

HERZOG, T.

- 2208 crassa

HITCHCOCK, A. S.

- 16950 macrophylla
17389 sessilifolia
17415 guianensis

HODGE, W. H.

- 6964 baccifera subsp. ferruginea

HOEHNE, F. C.

- 198 p.p. brasiliensis, p.p. micrantha

HOLT, E. G., and BLAKE, E. R.

- 537 macrophylla
599 japurensis
633 japurensis

HOLT, E. G., and GEHRIGER, W.

- 190 cayennensis
297 japurensis
302 japurensis
331 macrophylla
373 cayennensis

HOSTMANN, F. W., and KAPPLER, A.

- 162 angusta
438 cayennensis
1249 p.p. guianensis and p.p. pentagyna
1823 sessilifolia

HUBER, J.

- 92 reichardtiana
263 reichardtiana
1219 cayennensis
1479 baccifera subsp. subcuneata

HUMBOLDT, A. VON, and
BONPLAND, A.

- 676 guianensis
1038 cayennensis
1070 sessilifolia
1151 macrophylla
1152 baccifera subsp. dealbata
1715 lauriformis

IDROBO, J., and SCHULTES, R. E.

- 1199 confertiflora

JELSKI, C. DE

- 252 glabra subsp. pozuzoensis
253 jelskii (see Appendix I)

JENMAN, G. S.

- 977 angusta
4279 guianensis
5029 falcata
5035 macrophylla
5324 macrophylla
6278 guianensis
7017 p. p. falcata, p. p. sessilifolia

JOHNSON, W. M., and BARKLEY, F. A.

- 18C770 guianensis

JOHNSTON, J. R.

- 106 cayennensis

KALBREYER, W.

- 1374 angusta

KAPPLER, A.

- 1722 cayennensis

KAUFFMAN, E.

- 7 reichardtiana

KILLIP, E. P.

- 11734 sessilifolia
 34245 macrophylla
 34381 baccifera subsp. dealbata
 35453 sessilifolia
 35455 baccifera subsp. ferruginea
 37579 falcata
 38469 baccifera
 38480 lauriformis

KILLIP, E. P., BARKLEY, F. A., and
DANIEL, BRO.

- 39878 guianensis

KILLIP, E. P., and CUATRECASAS, J.

- 38976 panamensis
 39090 baccifera subsp. ferruginea

KILLIP, E. P., and SMITH, A. C.

- 14852 lauriformis
 15074 baccifera subsp. dealbata
 16335 baccifera subsp. dealbata
 19232 baccifera subsp. dealbata
 20037 baccifera subsp. dealbata
 25911 baccifera subsp. subcuneata
 26439 plicatifolia?
 26923 angusta
 27039 cayennensis
 27075 glabra
 27085 lateriflora
 27221 angusta
 27378 amazonica
 27541 sprucei
 27550 lateriflora
 27580 cayennensis
 27987 glabra
 28205 cayennensis
 29410 glabra
 29475 lateriflora
 29689 lateriflora
 30089 cayennensis
 30579 reichardtiana
 34340 guianensis

KLUG, G.

- 317 amazonica
 354 lateriflora
 745 sprucei
 888 angusta
 1009 glabra
 1524 amazonica

- 1861 confertiflora
 2263 tomentosa
 2344 minutiflora?
 3140 p.p. glabra, p.p. plicatifolia?
 3455 cayennensis

KRUKOFF, B. A.

- 1075 amazonica
 1175 amazonica
 1692 macrophylla
 4566 cayennensis
 4597 sprucei
 4735 angusta
 4946 cayennensis
 5241 glabra
 5946 amazonica
 6325 lateriflora
 6865 cayennensis
 6976 cauliflora
 7947 cauliflora
 8328 lateriflora
 8479 p.p. cayennensis, p.p. glabra
 8728 tomentosa
 10215 buchtienii
 11042 buchtienii
 12315 sessilifolia

KUHLMANN, J. G.

- 21223 lateriflora

LANG, H.

- 337 guianensis
 370 p.p. cayennensis, p.p. guianensis

LANG H., and PERSAUD, A. C.

- 286 sessilifolia

LANJOUW, J.

- 96 cayennensis
 344 guianensis
 398 angusta
 972 cayennensis
 1180 cayennensis

LANJOUW, J., and LINDEMAN, J. C.

- 1255 sessilifolia

LASSER, T.

- 1122 baccifera subsp. dealbata

LAWRANCE, A. E.

- 303 baccifera subsp. dealbata

LEHMANN, F. C.

- 2832 lauriformis
 3551 lehmannii
 4003 angusta
 5543 lauriformis
 5593 mandurr
 6617 mandurr
 7547 angusta
 7735 confertiflora
 BT450 lehmannii
 BT1086 lehmannii
 K74 lehmannii
 K75 mandurr

LINDEN, J.

- 13 lindeniana
 332 baccifera subsp. dealbata
 1502 baccifera subsp. dealbata

LINDER, D. H.

- 105 cayennensis

LITTLE, E. L., Jr.

- 6171 obtusa
 6330 obtusa
 7392 baccifera
 7617 mandurr
 7732 guianensis
 7982 mandurr
 8540 obtusa
 8727 baccifera subsp. ferruginea
 9783 macrophylla

LITTLE, E. L., Jr., and LITTLE, R. R.

- 7110 baccifera
 8252 japurensis
 8273 baccifera subsp. dealbata
 8275 urceolata
 8281 guianensis subsp. persicoides
 9501 baccifera subsp. dealbata
 9502 angusta

LOEFGREN, A.

- 91 reichardtiana

LUETZELBURG, T. VON

- 26248A martiana

MACBRIDE, J. F.

- 4089 sprucei
 4229 sprucei
 4574 glabra subsp. pozuzoensis

- 4763 glabra subsp. pozuzoensis
 5019 lateriflora

MACEDO, A.

- 2740 magnoliifolia

MAGUIRE, B.

- 23765 cayennensis
 23766 macrophylla

MAGUIRE, B., and STAHEL, G.

- 22779 cayennensis
 23624 cayennensis
 25053 japurensis

MALME, G. O.

- 2076 buchtienii

MARRERO, J. and LITTLE, E. L., Jr.

- 6274 panamensis

MARTIN, J.

- 27 latifolia

MARTIUS, K. F. D. VON

- 576 martiana
 970 micrantha

MATHEWS, A.

- 1309 baccifera subsp. subcuneata
 1310 p.p. glabra, p.p. glabra subsp. pozuzoensis
 1311 p.p. baccifera subsp. subcuneata, p.p. rusbyi, p.p. tomentosa

MAXON, W. R.

- 4774 viridiflora

McCARROLL, D.

- 99 rusbyi

METCALF, R. D.

- 30643 rusbyi?

METCALF, R. D., and CUATRECASAS, J.

- 30070 lauriformis

MEXÍA, Y.

- 4138 tomentosa
 4186 magnoliifolia
 4268 plicatifolia
 5981 reichardtiana
 5988 reichardtiana

6078 sprucei

6306 glabra

7084 confertiflora

7113 confertiflora

7153 obtusa

7167 obtusa

7760 tomentosa

8232 glabra

MIERS, J.

178 crassa

MOLINA, F.

15 guianensis

21 guianensis

MOORE, S.

137 buchtienii

609 buchtienii

MUTIS, J. C.

3718 baccifera subsp. baccifera

MYERS, J. G.

5764 amazonica

PENNELL, F. W.

1403 lauriformis

1674 baccifera subsp. ferruginea

3446 p.p. baccifera subsp. dealbata,
p.p. lauriformis

PENNELL, F. W., and KILLIP, E. P.

6298 baccifera

7263 lauriformis

8146 baccifera subsp. ferruginea

PENTLAND, J. B.

178 tomentosa

PÉREZ-ARBELÁEZ, E.

692 lehmannii

2534 baccifera subsp. ferruginea

PÉREZ-ARBELÁEZ, E., and
CUATRECASAS, J.

8168a baccifera subsp. ferruginea

PERSAUD, A. C.

16 japurensis

44 macrophylla

PHILIPSON, W. R., IDROBO, J. M., and
JARAMILLO, R.

2088 macrophylla

2092 baccifera subsp. dealbata

PICKEL, D. B.

3594 pentagyna

PINKUS, A. S.

166 japurensis

PIPER, C. V.

5763 viridiflora

5826 billbergiana

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2437 billbergiana

3876 billbergiana

4238 billbergiana

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WHITE, O. E.

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 966 tomentosa
 1144 tomentosa
 1205 angusta
 1385 angusta
 1460 angusta
 1533 angusta
 1639 glabra
 1734 angusta
 1748 angusta
 1793 lateriflora
 2061 glabra
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 2691 lateriflora
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18Ca063 lauriformis?

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U N I T E D S T A T E S N A T I O N A L M U S E U M

CONTRIBUTIONS FROM THE UNITED STATES NATIONAL HERBARIUM

VOLUME 35, PART 6

CACAO AND ITS ALLIES
A TAXONOMIC REVISION OF THE
GENUS THEOBROMA

By JOSE CUATRECASAS



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CACAO AND ITS ALLIES

A TAXONOMIC REVISION OF THE GENUS THEOBROMA

JOSE CUATRECASAS

Introduction

“Celebrem etiam per universam Americam multique usus fructum Cacao appellatum.”

CLUSIUS, 1605.

“Cacao nomen barbarum, quo rejecto Theobroma dicta est arbor, cum fructus basin sternat potioni delicatissimae, saluberrimae, maxime nutrienti, chocolate mexicanis, Europaeis quondam folis Magnatis propriae (βρωμα των θεων, Vos Deos feci dixit Deus de imperantibus), licet num vilior facta.”

LINNAEUS, Hort. Cliff. 379. 1737.

Theobroma, a genus of the family Sterculiaceae, is particularly noteworthy because one of its members is the popular “cacao tree” or “cocoa tree.” The uses and cultivation of this outstanding tropical plant were developed in the western hemisphere by the Mayas in Central America a long time before Europeans arrived on the continent. The now universally used name *cacao* is derived directly from the Nahuatl “cacahuatl” or “cacahoatl,” just as the name of the popular drink, chocolate, is derived from “xocoatl” or “chocoatl.” The economic importance of cacao has given rise to great activity in several fields of development and research, especially in agronomy. Historians and anthropologists have also been very much interested in learning the role played by cacao in the economy and social relations of the early American populations. There exists today an extensive literature devoted to the many problems related to cacao.

I saw cacao for the first time in Colombia in 1932, but became actually interested in the genus in 1939 and the years following, when I found cacao trees growing wild in the rain forests of the Amazonian basin. I was fascinated by the unique structure of the flowers of the cocoa tree, and its extraordinary fruit. My explorations from 1942

to 1947 at the service of the Government of the Valle del Cauca, mainly in the dense, humid forests of the Pacific coast of Colombia and western slopes of the Andes, offered me the opportunity to become better acquainted with wild species of *Theobroma*. I published the descriptions and illustrations of four new species found in that region, and at the same time gathered material for a monograph of the genus. Subsequently in Chicago and Washington I continued these studies, using the collections of the museums there and loans received from important European herbaria. The steadfast cooperation of V. M. Patiño has been of great value to me in several respects, and his explorations have furnished two new species. Jorge León from Turrialba sent me specimens of an outstanding new species. Collections sent to me for identification by the members of the English Colombian Cocoa Expedition (1952–1953) very much helped to broaden my knowledge of many of the species and their distribution. In 1954, I had the opportunity to study the important *Theobroma* collections at the British Museum (Natural History), London; the Royal Botanic Gardens, Kew; and the Muséum d'Histoire Naturelle, Paris, where many *Theobroma* types are preserved. In 1961 (July 11–15) I was allowed to examine several European collections, at that time on loan at the Harvard Botanical Museum, which I felt desirable to see before publishing this revision. On my way to Colombia in 1961 for a general collecting trip, I also visited the living *Theobroma* collection of the Imperial College of Agriculture in Trinidad where some 14 species and several hybrids and varieties are cultivated. I was thus able to supplement my data on the growing system and fruits of some of the species I had not seen living before. For the same purpose I visited the cacao stations of the Interamerican Institute of Agronomic Sciences at Turrialba, Costa Rica.

This publication is restricted to the taxonomy of the genus. Many binomials (see the index) have been published in the past, and there is great confusion with regard to the names in the herbaria and literature. A critical revision was necessary in order to establish the validity of the species and to list synonymy. Although a complete study of the genus would require much more exploration, because of the great gaps existing in the herbarium collections, the present revision of all available materials seems justified. Three critical treatments of the genus have previously been published; Bernoulli (1869) recognized 18 species, and Schumann (1886) 11. Chevalier, in 1946, acknowledged 13 species and a few subspecies; he united some species which should be held separate and on the other hand listed as different others which are actually synonyms. Twenty-two species are recognized in the present work. The number of species in the genus will probably increase in the future, because new explorations

in Central as well as South America will undoubtedly bring about the discovery of new ones.

This revision is based on the classical method of comparative morphology. I have to a large extent used the structure of the fruit and the vegetative characters which I found were basic features in the definition and taxonomy of *Theobroma*. For a better understanding of the genus, some new concepts are also contributed by G. Erdtman in pollen morphology (pp. 442–446), F. W. Cope in cytology and incompatibility in cacao (pp. 446–449), and by W. L. Stern in anatomy (pp. 439–442). These contributions may help in the understanding of the taxonomic problems of *Theobroma*, especially those derived from cultivated varieties. In regard to *T. cacao*, the classification of the various cultivars is provisionally presented in a conservative way; an understanding of the innumerable existing forms of cacao will only be possible after long-term genetic research. Dr. Cope and Dr. Bartley in Trinidad are working in this direction. Dr. Soria in Turrialba, Costa Rica, is engaged at this time in an ambitious project of this kind, largely supported by the American Cocoa Research Institute of Washington.

Due to the nature of this paper, the historical sketch is limited to the works which have contributed basic new data related to the taxonomy of *Theobroma*. The relationships with other groups and within the genus itself have so far as possible been treated objectively, with few hypothetical speculations. The specific descriptions are accompanied by original analytical drawings of the flowers, fruits, and leaves of almost all the species, and the illustrations, carefully supervised by the author, can be considered complementary to the written descriptions. Because of the relatively small number of existing collections, I think it useful to publish the information on herbarium specimens given by collectors; these data, except in special cases, have been translated into English whenever written in another language. However, the numerous herbarium collections of *Theobroma cacao*, mostly from cultivated plants, cannot be identified as to the variety and are therefore not included in the text but simply listed in the index. For the citations of herbaria the abbreviations of Lanjouw's "Index Herbariorum" have been used. The abbreviation Photo F.M. is used to indicate the photographic series of the Chicago Natural History Museum.

The artistic work for most of the illustrations has been carried out by the artists Christopher Reinecke, Maria Luisa Biganzoli, and Gil Cuatrecasas. Their work, consisting of about 35 plates, has been sponsored by the American Cocoa Research Institute; a few other plates had formerly been made by Gustavo Rojas, artist of the

Comisión Botánica del Valle, Colombia, and by Paula Gerard, Chicago.

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The collections used for this revision are the following:

- Arnold Arboretum, Harvard University, Cambridge, Mass. (A).
- Botanical Museum, Harvard University, Cambridge, Mass. (AMES).
- Botanisches Museum, Willdenow Herbarium, Berlin (B).
- Bailey Hortorium, Ithaca (BH).
- British Museum (Natural History) London (BM).
- Jardin Botanique de l'Etat, Bruxelles (BR).
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- Instituto de Ciencias Naturales, Bogotá (COL).
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- University of Glasgow, Dept. of Botany (GL).
- Systematisch-Geobotanisches Institut der Universität Göttingen (GOET).

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 Instituto de Biología, México (MEXU).
 Museu Goeldi de Historia Natural, Belem do Pará (MG).
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 Muséum d'Histoire Naturelle, Paris (P).
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 School of Forestry, Yale University, New Haven, Conn. (Y).

Historical Sketch

1605: First citation of cacao in botanical literature, by Charles de l'Ecluse (Clusius) in chapter XXVIII, of his *Exoticorum libri decem*, under the name *Cacao fructus*. It refers only to the fruit and gives a poor illustration of cacao seeds. "Celebrem etiam per universam Americam multique usus fructum Cacao appellatum."

1623: K. Bauhin mentions for the first time in his books in his chapter "Amygdalus" the cocoa plant as "Amygdalis similis Guatimalensis Avellana Mexicana cujus fructum indigenae Cacao appellant," etc. (Pinax Th. Bot. 442).

1630: The first prints of the Hernandez's *Rerum Medicarum Novae Hispaniae Thesaurus* appear in which are given descriptions of the cocoa tree under its Mexican name *cacahoaquahuatl* and of four varieties called *quauhcacahoatl*, *mecacahoatl*, *xochicacahoatl* and *tlalcacahoatl* which are distinguished by the fruits diminishing in size from the first to the last, presumably representing cultivars; the pods were called *cacahoacentli* and the useful seeds *cacahoatl*; he also mentions *quauh-patachtli* which undoubtedly refers to *Theobroma bicolor*. His illustration of the first (fig. 223) is clearly cacao Criollo.

1658: W. Piso describes cocoa "De Arbore Cacavifera" and repeats the varieties cited by Hernandez in a long article on cocoa and chocolate. His drawing also represents the Criollo variety.

1688: John Ray, in his *Historia Plantarum*, gives much attention to cacao and its products in chapter VIII under the title: *Cacao* Ger. *Cacao sive Cacavate* Park. *Cacao Americae sive Avellana Mexicana* J. B. *Amygdalae similis Guatimalensis* C. B. *The Cacao Tree*. He explains that there are four kinds of cocoa trees and under the heading of *Cacava quahuatl* describes the tree, fruits, and seeds which he compares to almonds saying that they are white before ripening and red when fully ripe.

1696: Plukenet, in his *Almagestum Botanicum*, classifies cacao as an almond, under the name *Arvor cacavifera Americana*, the fruits of which (folliculi) contain some kind of almonds; in his plate 268, fig. 3, a leafy branch with a cacao fruit of the Criollo variety is represented.

1696: Sloane lists *Cacao* in his catalog of Jamaican plants, with a long series of quotations from previous authors and travel writers.

1700: The first taxonomic statement is made by Tournefort publishing the genus *Cacao*: "*Cacao est plantae genus auctore clariss. Plumerio*" with a single species "*speciem unicam novi*." He gives a short description and drawings sent to him by Plumier. They distinguish the 5 sepals, the strangulated petals, and a pistil surrounded by a laciniate girdle (staminodes) which develops into a ridged and pointed fruit filled with seeds.

1705: Sibilla Merian gives an illustration of Surinam cacao which proves to represent clearly the Criollo type (26, t. 26).

1710: Ray in his *Methodus Plantarum* copies Tournefort's description and data to define *Cacao*; there are no changes in the 1733 edition.

1725: Sloane publishes a long article on "The Cacao Tree" in his *Voyage to Jamaica* (vol. 2) giving the following botanical description (p. 15): "Out of the Body of the Tree, or Branch comes a very small Flower, standing on a half Inch long Footstalk, it is made up of 5 *Capsular* Leaves, 5 crooked Petals, several *Stamina*, and a Stylus, of a very pale Purple color, after which follows the Fruit, which when ripe is as big as one's Fist, bigger in the Middle than at the Ends, which are pointed, it has some *Sulci* and *Asperities* on its Outside, is for the most Part of a deep Purple colour, the Shell being about Half a Crown's thickness, and containing within it many Kernels of an oval Shape, each of which is as big as a *Pistachia* Nut, having a thin Membrane without which is a mucilaginous Substance in which it lies. The Nuts themselves are made up of several parts like an Ox's Kidney, some Lines being visible on it before broken, and is hollow within, its Pulp is oily and bitterish to the Taste, made up of many *Striae*, which tend from the Circumference to the Center." The plate 160 illustrates a leafy branch with oblong-ovoid fruits, 10-ridged and strongly pointed; there are separate drawings of flowers

showing more or less clearly 5 sepals, some petals and (not well defined) 4 or 5 staminode lacinae at the center, but no stamens; seeds, one isolated, some others together covered with pulp are also illustrated. The article gives much information about cultivation, varieties, geographical distribution, and trade in cocoa, and many authors are cited.

1737: Linnaeus (*Genera Plantarum*) introduces cacao into *Classis* 18 of his classification, in *Polyadelphia pentandria* giving it a new name *Theobroma*—meaning “food for the Gods”; the name *Cacao* given by Plumier and Tournefort was rejected by Linnaeus as “barbarous.” By the International Code of Botanical Nomenclature, Linnaeus’ name prevails. The new genus *Theobroma* was published almost at the same time in the *Genera Plantarum* and in *Hortus Cliffortianus*; Linnaeus described the flowers as having 5 stamens, 5 petals and staminodes (*folioli nectarii*), but only 3 sepals and with 5-celled anthers instead of 4. Linnaeus probably used dried specimens and annotations sent to him by Sloane for his description. He included in *Theobroma* two species: one with “*foliis integerrimis*,” *Cacao*, the other with “*foliis serratis*,” *Guazuma*, both also differentiated by their fruits. In the *Genera Plantarum*, he gives as the only synonyms and citations Tournefort for *Cacao* and Plumier for *Guazuma*, but in the *Hortus Cliffortianus* he quotes for *Cacao*: *Clus.*, *Raj.*, *Tourn.*, *Sloane*, *Mer.*, *Hern.*, *Pluk.*, and *Bauh.* But Linnaeus found out by himself, with the help of Sloane, the number and kind of stamens typical of *T. cacao*. He writes in *Hortus Cliffortianus*: “*Flores a nullo bene depicti, multo minus descripti sunt*,” and then: “*Sloane mihi inspiciendi copiam fecit, videbatur structura exacte sequentis, ab aliis in universum omnibus diversissima.*” His original description of the stamens, given in the *Genera Plantarum* (“*Filamenta subulata, longitudine nectarii, cui radiorum instar innata: singula apice quinquefida. Antheris in singulo stamine quinque, tectis petalo concavo*”), was made on the basis of drawings or flowers sent to him by Sloane, for which reason the flowers of the Sloane herbarium have to be considered as the type of Linnaeus’ description. But Linnaeus may have had very scanty material of the flowers, because he described the anthers as 5-celled instead of 4-celled.

1739: Weinmann writes extensively about cacao and chocolate and gives a plate (277) which is inspired by Tournefort’s illustration using very much imagination in painting it. Plate 278, devoted to *Cacao minor*, depicts a very deformed kind of pod.

1739: Elizabeth Blackwell depicted cacao (*pl.* 373) using Miller’s specimens and suggestions. The fruit is figured as elongate, pointed

and 10-ridged, although slightly verrucose; it represents the Criollo type.

1741: Geoffroy in his *De Vegetabilibus Exoticis* has a long article (XIX) *De Cacao* giving detailed descriptions of the tree, fruits, seeds, and their preparations. He calls the attention to the variability of the species in size or thickness of the different organs (especially the leaves and fruits).

1747: Catesby publishes a magnificent colored plate of the cocoa tree in his Appendix to the Natural History of Carolina, etc. (p. 6, pl. 6); the buds are colored red, the petals yellow, the staminodes red, and the fruits orange, obovoid-oblong, 10-ridged and warted, and very pointed; clearly it is the Criollo type. There is a long description of the tree with observations taken from Dampier; of the fruit it is said: "Fruit about the bigness of a swan's egg, but longer, more tapering, and ending in a point. The fruit hangs pendant, and when ripe, has a shell of a purple color, in substance somewhat like that of a pomegranate, and furrowed from end to end, containing in the middle many kernels of the size of acorns, inclosed in a mucilaginous substance . . ." In a later edition (1771) the color of the fruit was changed to dark violet.

1749: Linnaeus, in his *Materia Medica*, includes *Theobroma foliis integerrimis* (p. 364) with the previous definition and classification; he attributes to it the qualities and virtues of *pinguis*, *subamara*, *nutriens*, *aphrodisiaca*, *calefaciens*.

1753: Linnaeus gives a binomial name to cacao in his first edition of the *Species Plantarum* (p. 782): *Theobroma Cacao*, with the short specific diagnosis "*foliis integerrimis*." He also names a second species *Theobroma Guazuma* with the diagnosis "*foliis serratis*." To the bibliographical citations are added: "*Mat. Med.* 364," "*Geoffr. Mat.* 409," and "*Catesb. car.* 3. p. 6. t. 6." Inasmuch as the first edition of Linnaeus' *Species Plantarum* is the official beginning publication date for phanerogams by the Code of Nomenclature, *Theobroma cacao* receives here its official nomenclatural start, the generic name being in accordance with the diagnosis given in the corresponding edition (fifth) of Linnaeus' *Genera Plantarum*.

1754: Linnaeus, in the fifth edition of *Genera Plantarum*, defines *Theobroma* and gives it the same classification (Polyadelphia pentandria) as in the first edition. Linnaeus did not improve his knowledge of the genus nor change his concepts of it in later works. In the third edition of *Species Plantarum* (1764), and also in the twelfth edition of *Systema Naturae* (2: 508. 1767) he keeps the same treatment of *Theobroma* as in his earlier publications.

1754: The generic name *Cacao* is validated, according to the present Code of Nomenclature, by Miller in his fourth abridged edition of

"The Gardeners Dictionary." As in his popular sixth (1752) and eighth (1768) and other later editions of the Gardeners Dictionary, Miller publishes, without or with slight variations, a long article on "Cacao," "The Chocolate Nut." He explains that "This genus of plants was constituted by Father Plumier, who communicated the characters, which he had drawn in America, to Dr. Tournefort, who has inserted it in the Appendix of his Institutions. Dr. Linnaeus has joined this to the *Guazuma* of Plumier, under the title of *Theobroma*, but as the fruits of these plants are very different from each other, I shall keep them under different genera. We have but one species of this plant, which is Cacao."

1763: Adanson separates *Cacao* (*Theobroma*) from *Guazuma*, but, while the latter is kept in the family "Les Tilleuls," *Cacao* is placed in the family "Les Pistachiers," side by side with *Diosma*, *Triopteris*, *Acaju*, *Hugonia*, etc., far away from its true relationships.

1765: A disciple of Linnaeus, Antonius Hoffmann, presents to the Swedish Royal College of Medicine the first doctoral thesis ever proposed dealing with a *Theobroma* subject, "Potus Chocolatae." It is an excellent review of the knowledge about the composition and ways to prepare the chocolate at that time and the nutritional and medical importance of it. Hoffmann gives a more detailed description of the cacao plant and the fruit than did Linnaeus, probably inspired in Geoffroy; he writes: "Fructus magnitudinem et figuram refert Melonis, sed verrucosus est, decem angulis instructus et superne acuminatus; dum maturescit, fit colore coccineus atque maculis variegatus flavis; intus continet nucleos circiter triginta, qui magnitudine Olivas aemulantur ac *pulpa* obteguntur albida, subdulci et amaricante. Olei magna scatent hic nuclei copia, quod expressum vocatur *Pinguedo de Cacao*." (1769, p. 257.)

1775: A disciple of Linnaeus, Jacobus Alm, in his doctoral dissertation *Plantae Surinamenses* republished ten years later in *Amoenitates Academicae*, emends the Linnaean description of the cacao flowers. He recognizes sterile stamens ("stamina alia 5, castrata") in what Linnaeus called "nectaria," alternate with the other "stamina fertilia solitaria"; he corrects Linnaeus also in seeing the calyx "pentaphyllus" and the anthers "quadriplici."

1775: Aublet, in his explorations in French Guiana, found wild species of *Theobroma*, which he describes extensively in his *Histoire des Plantes de la Guiane*. He names them *Cacao guianensis* (pl. 275) and *Cacao sylvestris* (pl. 276); he quotes "cacao" as a Caribbean name used. To the cultivated cacao, which he also found, he gives the new name *Cacao sativa*. It is unfortunate that Aublet mixed up elements of three species in describing his two new species; *Cacao sylvestris* was pictured from concordant parts of foliage and fruits

which agree well with the species at present known as *T. subincanum*, but the flowers mentioned in his description were from *T. cacao*. *Cacao guianensis* was described and depicted from branches and foliage identical to *Cacao sylvestris* (= *T. subincanum*) and its flowers were taken from specimens of *T. cacao*; the fruit is the only different part, belonging to a third species. Aublet's descriptions and drawings are detailed, this being the first publication giving an accurate idea of the cacao flowers and of the fruits of some wild *Theobroma*.

1785: Lamarck, in his famous *Encyclopédie Méthodique*, lists *Cacao* as belonging to the family of *Cacaoyers* characterized by hermaphrodite and complete flowers with 5 petals, 5 or 10 stamens and superior, usually 5-celled ovary; other genera of the family were: *Ambroma*, *Guazuma*, *Ayenia*, *Buttneria*, and *Kleinhovia*. He points out its close relation to *Hermannia*, *Tilia*, and the *Malvaceae*. He describes three species: *Cacao sativa*, *C. sylvestris*, and *C. guianensis* with the remarks mostly taken from Aublet.

1789: A. L. Jussieu (*Genera Plantarum*) places *Theobroma* in *Classis XIII*, *Ordo XIV* (*Malvaceae*), of his system including it in his section V, (bis!) characterized by mixed fertile and sterile stamens connate at base; here *Theobroma* is associated with *Pentapetes* L., *Abroma* Jacq., *Guazuma* Plum., *Melhania* Forsk., *Dombeya* Cav., *Assonia* Cav., and *Byttneria* L.

1791: Gaertner, in his remarkable book on fruits and seeds, gives a good description of cacao and drawings of its fruits and seeds, which represents a Criollo form; undoubtedly, Gaertner had at hand a dried specimen, for the section of the pod is drawn relatively thin and he describes it with "cortex sublignosus." The specific name used by Gaertner, *Cacao minus*, is a nomenclatural synonym of *Theobroma cacao*; Gaertner mentions *Theobroma foliis integerrimis* Linn., besides Sloane and Blackwell.

1791: Schreber, in the eighth edition of Linnaeus' *Genera Plantarum*, divides *Classis XVIII* in two subclassis, *Decandria* and *Dodecandria*. He places *Theobroma* in *Decandria*, a new concept, while *Bubroma* (a new name for *Guazuma*) and *Abroma* are brought into the *Dodecandria*. Schreber points out as differences between *Theobroma* and *Bubroma*, that the first has "laminae subrotundae acuminatae" and "antherae in singulo filamento duae," while *Bubroma* has "laminae semibifidae," "antherae in singulo filamento tres," and "capsula non dehiscens muricata."

1791: Gmelin, in the 13th edition of Linnaeus' *Systema Naturae* (vol. 2, p. 1151), includes *Theobroma* in *Polyadelphia Decandria* together with the genus *Abroma*. He still lists *T. Cacao* and *T. Guazuma* as species of *Theobroma*, adding another: *Theobroma guianense*, a new combination based on Aublet's *Cacao guianensis*.

1796: Salisbury publishes *Theobroma celtifolia*, which is a synonym of *Guazuma ulmifolia*.

1796: Lamarck (Tableau Encyclopédique) publishes illustrations of *Theobroma Cacao*, fig. 1 representing flowers, copied from Aublet's plate, fig. 2 the smaller form of *T. cacao* illustrated by Gaertner, and fig. 3 a correct drawing of flowering and fruiting branches of a Criollo cacao (not *T. guianense* as stated).

1802: Willdenow, in his edition of Linnaeus' Species Plantarum, follows the treatment of Schreber, including *Theobroma* in Polyadelphia Decandria and *Bubroma* and *Abroma* in Dodecandria. Still only two species are considered: *T. cacao* and *T. gujanensis*.

1806: Humboldt and Bonpland, in Plantae Aequinoctiales, a magnificent work, publish the first perfect botanical description of a species of *Theobroma*. It is supplemented with two plates illustrating leafy and flowering branches, fruits, seeds, and flowers of *Theobroma bicolor*, found by the authors cultivated in Colombia. The drawings show details of the embryo; the staminodes are wrongly figured as pointed instead of obtuse.

1808: De Tussac, in Flora Antillarum, writes extensively on the cacao tree, its cultivation and uses, under the heading *Cacao Theobroma*, giving "Le Cacaoyer Theobrome" as the French and "The Chocolate Tree" as the English name. There is a plate in folium (pl. XIII) showing illustrations of orange yellowish, 10-ridged fruits, attenuate at both ends, foliage, floral details, and the embryo. De Tussac is so enthusiastic about the use of chocolate that he says "le chocolat est au corps, ce que le café est à l'esprit" (p. 103).

1811: Poiret, in the supplement to Lamarck's Encyclopédie, makes the new binomial *Cacao bicolor*, a combination based on the Humboldt and Bonpland species.

1812: Stokes, in his Botanical Materia Medica, publishes a new name, *Theobroma integerrima*, for *T. cacao* L.

1823: Kunth, in Humboldt, Bonpland, and Kunth, Nova Genera et Species Plantarum, gives a good description of the genus *Theobroma* and of the two species *T. cacao* and *T. bicolor*; the description of the androecium is entirely correct: "Filamenta 10, basi in urceolum connata; quinque petalis opposita dianthera; quinque alterna sterilia, lineari subulata. Antherae didymae biloculares, in petalorum cavitatae reconditae." Kunth gives a good description for the family Büttneriaceae R. Brown and for the five sections in which it is divided (Sterculiaceae, Büttneriaceae verae, Lasiopetaleae, Hermanniaceae and Dombeyaceae). *Theobroma* (jointly with *Guazuma*, *Abroma*, *Glossostemon*, *Büttneria*, *Ayenia*, and *Commersonia*) are placed in the Büttneriaceae verae which have the stamens "10-30. Filamenta magis minusve connata; quinque, laciniis calycinis opposita,

antheris destituta, alius formae. Antherae didymae, longitudinaliter dehiscentes."

1824: De Candolle, in his *Prodromus*, accepts also family status for the Byttneriaceae (as Ordo XXVI) and follows the classification of Kunth, except for calling the sections divisions. In the tribe Byttneriaceae he includes the same seven genera, plus another doubtful one. In his treatment of *Theobroma* he includes five species, three already known, *T. cacao*, *T. guianensis*, and *T. bicolor* and two new ones, taken from the Mexican flora of Mociño and Sessé: *T. angustifolia* and *T. ovatifolia*. Mociño and Sessé had written an unpublished Flora of Mexico supplemented by a series of illustrations, which were copied at Geneva by artists hired by De Candolle.

1826: Sprengel, in the sixteenth edition of Linnaeus' *Systema Vegetabilium*, keeps *Theobroma* in Polyadelphia (Classis XVIII) and divides it in three genera: *Theobroma* with 2-antheriferous stamens and *Bubroma* and *Abroma* with 3-antheriferous stamens. He lists five species in *Theobroma*: *T. cacao*, *T. bicolor* Humb., *T. speciosum* W. herb., *T. ovatifolium* Sess., and *T. guianense* W. The genus *Bubroma*, considered synonymous with *Guazuma* Poir., comprises five species: *B. Guazuma*, *B. tomentosum*, *B. polybotryon* W., *B. grandiflorum* W. herb., and *B. Invira* W. Of these *B. grandiflorum* is actually a *Theobroma*. In *Abroma*, Sprengel included two species: *A. augustum* L. suppl., and *A. fastuosum* Salisb. New *Theobroma* species in this publication are *T. speciosum* and *B. grandiflorum*.

1827: Descourtilz, in his picturesque *Flore Médicale des Antilles*, dedicates much space to the description of the cacao tree "Cacaoyer cultivé," to its origin, cultivation, varieties, uses, etc. Plate 266 represents a leafy branch with flowers, seeds, and a fruit which is of the Criollo type (10-ridged, very warty, and acute).

1828: Voigt publishes a description of a *Theobroma guianensis* without mention of *Cacao guianensis* Aublet ("fol. acuminatis cordatis sublobatis inaequaliter eroso-dentatis, subtus tomentosis, ramis petiolisque ferrugineo-hirtis, corymbo terminali. Flores albi, parvi). According to some of the features given (corymbo terminali, flores albi), the plant described does not belong to *Theobroma*.

1830: Sweet, in *Hortus Britannicus*, listed four species under *Theobroma* mentioning a new binomial, *T. caribaea*, with no description. It is undoubtedly a name for a form *T. cacao*.

1830: Martius, who observed and collected many *Theobromas* on his trips throughout Brazil, says that more species may be found growing wild in tropical forests; he gives an account with short descriptions of the species found by him in Brazil, of which three are new species: *Theobroma subincanum* Mart., *T. sylvestre* Mart., and

T. microcarpum Mart.; the other species listed are *T. cacao* L. (= *T. sativum* Lam.), *T. speciosum* Willd. ?, and *T. bicolor* H. et B.

1831: Don, in A General History of the Dichlamydeous Plants, places *Theobroma* in the family Byttneriaceae, tribe Byttnerieae DC. He gives good descriptions of these groups and of *Theobroma*, and short definitions for six species with some special attention to *T. cacao*. The other species listed are: *T. guianensis*, *T. bicolor*, *T. angustifolia*, *T. ovatifolia*, and *T. sylvestris*, the last being a new combination for *Cacao sylvestris* Aubl.

1831: Martius, in his Reise in Brasilien (p. 1127), explains that the cocoa from Pará and Rio Negro is of a lower, more bitter quality, because it comes more often from wild cacao trees than from cultivated trees. He also says that he found *T. bicolor* growing wild in Barra do Rio Negro, in Manacurú, and Yapurá.

1840: Endlicher, in his Genera Plantarum, gives excellent descriptions for the Ordo CCXI Büttneriaceae and its six tribes, two of them being new: Eriolaenae and Philippodendrae; the other four are the same as those of Kunth and De Candolle, except for the Sterculiaceae which are treated as an order apart united with Bombacaceae and Helicteraceae. He includes in Büttnerieae DC. the genera *Rulingia*, *Commersonia*, *Abroma*, *Büttneria*, *Ayenia*, *Theobroma*, and *Guazuma*. The genus *Glossostemon* is placed in the Dombeyaceae.

1847: Dietrich, in his Synopsis Plantarum, describes briefly nine species of *Theobroma* and gives a new name, *Theobroma Martiana*, for *T. sylvestris* Mart.

1856: Karsten describes *Theobroma glaucum*, a new species from eastern Colombia.

1861–1870: Baillon studies the development of the parts of the flower in *T. cacao*. The primordia of the sepals appear successively one after another, emerging above a common basal annulus. The petal primordia appear simultaneously and have the same aspect as in flowers of most other plants, but when they develop, there appears a strangulation which divides them into two articulated parts; the basilar parts are valvate, the upper parts contorted. The staminode primordia, opposite to the sepals, appear before those of the fertile stamens, which are opposite to the petals, and develop a simple filament which divides into two, each branch having an anther whose two thecae become superimposed. The five primordia of the carpels opposite to petals have a half-moon shape; they become connate and develop alternate growths at the joints which are the primordia of the walls; these are centripetal and progressively divide the ovary into five cavities. Primordially, the placentation is parietal, becoming axile when the carpelar walls reach the axis; the ovules develop two integuments, become anatropous and placed in two rows in each

cavity, with the raphe, outside facing each other, horizontal. The embryo at first has ovate-orbicular entire, flat cotyledons; later these develop folds becoming corrugated. The initial transparent albumen is absorbed and at the end disappears.

1862: Triana and Planchon, in *Prodromus Florae Novogranatensis*, list three species of *Theobroma* for Colombia (*T. cacao*, *T. bicolor*, and *T. glauca*) and three species of *Herrania* (*H. pulcherrima*, *H. albiflora*, and *H. laciniifolia*). *T. cacao* is only given as cultivated.

1862: Bentham and Hooker (*Genera Plantarum* 1:ix, 216), following basically the lines of De Candolle, although using other terms, classify *Theobroma* in the series Thalamiflorae, cohors VI Malvales, ordo XXXII Sterculiaceae and tribus VI Buettnerieae. The chief characters for the tribe are the hermaphrodite flowers, concave petal base, and anthers 1-3 alternating with staminodes; it is divided into two groups: *) the fertile stamens with 2- ∞ anthers (*Glossostemon*, *Abroma*, *Theobroma*, *Herrania*, *Guazuma*), **) the fertile stamens with a single anther (*Ayenia*, *Buettneria*, *Rulingia*, *Commersonia*). With the main characters of most of the genera already known, good defining descriptions are given for each of them.

1869: Bernoulli attempts the first monograph of *Theobroma*. After a long time of field study in Central America and using the herbarium collections preserved at Berlin, Kew, and Munich, Bernoulli became so well acquainted with the genus that he was able to draw a very good natural classification of it. The five sections established by him, based on flower and fruit characters, may be entirely kept today, strongly reinforced by other more recently known characters. When he started the study, there were only four or five species known besides *T. cacao*; and he writes, "Actually nobody knew these species, because the extremely short diagnoses of the old species were completely insufficient to determine them, for which reason there was the greatest confusion in the nomenclature in the herbaria that I had the opportunity to see." Bernoulli found that flowers and fruits give constant characters, whereas the leaves only give some secondary characters, especially the basal nervation; he also noticed that in some species there is great variation in the shape and pubescence of the leaves, with all transitions from one to another form when abundant material is compared. The basic characters used by Bernoulli for his system are: petal appendix or ligula sessile, subsessile or stipitate; staminodes erect or reflexed in bud, subulate, claviform, or petaloid; stamens 2-antheriferous or 3-antheriferous; fruit, when it was known; calyx 5- or 3-parted with narrow or broader lobes. With combinations of these features the following five sections (the descriptions here abridged) result.

1. *Cacao*: Petal ligule stipitate; staminodes erect, subulate; stamens 2-antheriferous; calyx 5-parted, the laciniae equal. Fruit ovate-oblong.
2. *Oreanthes*: Petal appendix subsessile; staminodes erect, subulate; stamens 3-antheriferous; calyx 5-parted, the laciniae equal.
3. *Rhytidocarpus*: Petal appendix subsessile; staminodes erect, claviform; stamens 2-antheriferous; calyx 5-parted, the laciniae equal; fruit woody.
4. *Telmatocarpus*: Petal ?; staminodes erect ?, linear-subulate with broad base; stamens 3-antheriferous; calyx 5-parted, the laciniae equal; fruit ovate, lacunose.
5. *Glossopetalum*: Petal ligule stipitate; staminodes reflexed, petaloid; stamens 3-antheriferous; calyx irregularly 3-5-fid, "foliaceous"; fruit sublignose.

Bernoulli describes 18 species, some of them extensively, others very briefly, according to the material he had at his disposal. Of these, 12 species are described as new. In sectio *Cacao* he includes 4 species: *T. cacao* L. and 3 new ones: *T. pentagona*, "cacao lagarto" from Guatemala; *T. leiocarpa*, "cumacaco" from cultivation in Guatemala; and *T. saltzmanniana* from Bahia, Brazil. In sectio *Oreanthes* he includes *T. speciosa* Willd. ex Spreng., and 2 new species: *T. quinquenervia* and *T. spruceana*, both from Brazil. Sectio *Rhytidocarpus* with one species, *T. bicolor* Humb. & Bonpl. (synonym, *T. ovatifolia* DC.), and, as doubtful, also *T. glauca* Karst. In sectio *Telmatocarpus* there is a single species, *T. microcarpa* Mart. In the sectio *Glossopetalum*, the largest, he describes in some detail *T. angustifolia* DC., *T. subincana* Mart., *T. sylvestris* Mart., and as new species *T. macrantha* from Brazil, *T. ferruginea* from Peru, *T. obovata* from Brazil, *T. alba* from British Guiana, and *T. nitida* from Brazil. About "Cacao guyanensis" Aublet, he writes "bleibt somit eine vollstandig ungewisse Art. Sie scheint auch von keinem weiteren Autor gesehen worden zu sein, sondern immer nur nach Aublet citiert zu Werden." Bernoulli quoted *Herrania* as a genus differing from *Theobroma* in the habit of the plant and in the 5-6-foliolate digitate leaves. Bernoulli's work is illustrated with several drawings. This monograph was published by the Swiss Society for Natural Sciences in its new serial of Memoires, vol. 24, no. 3, in 1871. However, a reprint was issued previously in pamphlet form in 1869, which is the effective date of publication. (See Pritzel, 1872; Sargent, 1912). C. G. Bernoulli was born in Basel, Switzerland, Jan. 24, 1834, and died in San Francisco, Calif., while returning home, May 18, 1878; he lived in Guatemala from 1858 until 1878 and collected plants and animals extensively in Central America.

1873: Baillon publishes excellent comparative descriptions of the genus based on *T. cacao* in his Histoire des Plantes. He includes it in the family Malvaceae which includes the Sterculiaceae and Bomba-

caceae; the family is divided into twelve series, the sixth being the *Buettnerieae* with 12 genera: *Buettneria*, *Ayenia*, *Commersonia*, *Rulingia*, *Theobroma*, *Herrania*, *Guazuma*, *Scaphopetalum*, *Leptonychia*, *Abroma*, *Maxwellia*, and *Glossostemon*. The main characters given for the tribe are the usually hooded petal base, the fertile stamens opposite the petals, the staminodes alternate with the petals, the bilocular anthers (rarely 3-locular), the plurilocular ovary, and the capsular or carnose fruit.

1882: D. Morris of Jamaica, in his well-known book on cultivation of cacao, after describing the cacao plant and fruit, publishes the first known classification of its varieties based upon the nomenclature of some of the best estates of Trinidad. He distinguishes two great classes (p. 12), the second being divided into several varieties:

Class I. Cacao Criollo (Red).

Class II. Cacao Forastero.

var. *a.* Cundeamor verugoso amarillo (yellow), (rough yellow Cerasee)

b. Cundeamor verugoso colorado (red), (rough red Cerasee)

c. Liso amarillo (yellow), (smooth yellow)

d. Liso colorado (red), (smooth red)

e. Amelonado amarillo (yellow), (yellow Melon)

f. Amelonado colorado (red), (red Melon)

g. Calabacillo amarillo (yellow), (yellow Calabash)

h. Calabacillo colorado (red), (red Calabash)

This is the first valid publication in the nomenclature of the cultivars of *Theobroma cacao*. Morris goes on to say that before the "blast" or plague that almost exterminated cacao plantations in Jamaica before the end of the seventeenth century, the Criollo class was the only kind cultivated there. Since then, the Criollo has been entirely discarded for the hardier Forastero, the Criollo being "now chiefly confined to the mainland (Venezuela) where its yield, though small, is considered of great value" (p. 13). This assertion determines that the nomenclatural type of the Criollo cultivar is the Venezuelan Criollo. Of the Forastero varieties the best are the Cundeamor, the yellow kind being preferred for yielding a larger proportion of seeds. The seeds of Cundeamor "are mostly of the true almond shape—large, plump and full, of a pale crimson colour in the interior, and ferment easily." The Liso variety is closely allied to the former. The Amelonado is intermediate between Cundeamor and Calabacillo, and is considered as of good quality. The Calabacillo is the lowest quality and, Morris says, "never cultivated by a judicious planter; its fruits are small, the seeds flat, angular, intensely bitter and of dark crimson colour."

1886: Schumann, in his *Vergleichende Blütenmorphologie*, makes an accurate morphological analysis of eleven genera of Büttnerieae,

especially of *Büttneria*, *Ayenia*, *Commersonia*, *Rulingia*, *Guazuma*, *Theobroma*, and *Abroma*, and tries to figure out the existing relationships between them and other Sterculiaceae genera. He concludes that the genera treated have a very close relationship and constitute a very natural group. Schumann sees in the Sterculiaceae two series, one of which is the main series (Hauptreihe), with a floral diagram $C_5, P_5, Std_5, A_5, G_5$, where P.A.G. are opposite; these elements are either normally developed or modified by division or abortion; to this series belong as the leading tribe, the Büttnerieae, followed by Sterculieae, Helictereeae, Lasiopetaleae and part of Hermannieae (*Melochia*, *Dicarpidium*, *Waltheria*). The other division of the Sterculiaceae differs in having a floral diagram with the carpels opposite the sepals, this includes the Dombeyeae and *Hermannia*. He sees very close relationships between Büttnerieae and Lasiopetalae, which have to be artificially separated, and also between *Büttneria* and *Ayenia*, between *Theobroma* and *Guazuma*, and between the last and *Scaphopetalum* and *Leptonychia*. There is no direct relationship between the two series of the Sterculiaceae, the Dombeyeae being close to the Malvaceae. Schumann does not see a way to explain this and decides not to draw any evolutionary hypotheses.

Schumann describes the calyx of *Theobroma* as pentamerous or with three divisions, the sepals often concave and slightly cucullate, the petals sessile or shortly unguiculate. The inner glands of the receptacle are pluricellular and stipitate-globose or flagelliform; their function is unknown. The staminodes are more or less carnose. The ovules are in 2 rows in the ovary cells, but the seeds become uniseriate. The pulp of the seeds is mucilaginous and includes fine, curled, spiralish fibres.

1886: Schumann, in the Flora Brasiliensis, gives a synopsis of *Theobroma*, describing with detail and accuracy its recorded species. But he does not follow the well-based system of Bernoulli. Schumann includes the genus *Herrania* in *Theobroma* as section *Herrania*, leaving the other species as section *Eutheobroma*. He uses the shape of the petal lamina and the staminodes and the number of anthers in a single stamen as secondary characters to classify the species using as the primary character the many-flowered or few-flowered inflorescence, a very vague feature in many instances. The keyed species in the first group are *T. Cacao*, *T. bicolor*, and *T. speciosum*, and in the second group, *T. microcarpum*, *T. grandiflorum*, *T. subincanum*, and *T. angustifolium*. Four species are listed outside of the key as "dubiae": *T. glaucum* Karst., *T. silvestre* Mart., *T. Martii* Schum., and *T. album* Bern. Two excellent illustrations are given for *T. Cacao* and *T. grandiflorum*. Schumann reduces to *T. Cacao* three Bernoulli species, *T. leiocarpum*, *T. pentagonum*, and *T. salzmännianum*, which

he thinks were based on insignificant variations of fruits or petals of this polymorphic species. Also he considers the flowers of *Cacao guianensis* Aublet as being *T. Cacao*, whereas the foliage and fruit is possibly *T. subincanum*. Bernoulli's *T. quinquenervium* and *T. spruceanum* are reduced by Schumann to varieties of *T. speciosum*. Schumann transfers *Bubroma grandiflorum* Willd. to *Theobroma*, citing as a synonym *T. macranthum* Bern. *T. obovatum* Kl. ex Bern. was not well known to Schumann, who makes it a synonym of *T. subincanum*. In short, the 18 species listed by Bernoulli are reduced by Schumann to 11, four of these being dubious to him.

Schumann places *Theobroma* in the family Sterculiaceae, tribe IV Büttnerieae, characterized mainly by cucullate petals. This is divided into two subtribes, corresponding exactly to the two groups made by Bentham and Hooker, but Schumann gives them names: a) *Theobrominae*, defined as having 10 or 15 stamens and the base of petals cymbiform, and b) *Büttnerinae*, distinguished by having 5 stamens and the petal cucullus incurved at apex. *Theobroma* is the principal genus of the first, differing from *Guazuma* by its baccate fruit, lack of perisperm, and scarce, mucilaginous endosperm; *Guazuma* has lignose fruits, a developed perisperm, and lacks endosperm.

1890: Schumann in his treatment of the Sterculiaceae for Engler and Prantl's *Die Natürlichen Pflanzenfamilien* divides *Theobroma* into three sections: 1) *Herrania*, 2) *Eutheobroma* (2-antheriferous stamens) with *T. cacao* and *T. bicolor*, and 3) *Bubroma* (3-antheriferous stamens) with *T. angustifolium*, *T. ovatifolium*, *T. grandiflorum*, and *T. subincanum*. There are good illustrations. Schumann divides the family into eight tribes, *Theobroma* belonging to the fifth, Büttnerieae, characterized by hooded petals. It is divided into subtribe Büttnerinae with single stamens and *Theobrominae* with bundled stamens; the first includes *Rulingia*, *Commersonia*, *Büttneria* and *Ayenia*, and the second *Glossostemon*, *Scaphopetalum*, *Leptonychia*, *Abroma*, *Theobroma*, and *Guazuma*.

1890: Gómez de la Maza publishes *Theobroma tomentosa*, based on *Guazuma tomentosa*.

1892: Hart modifies the Morris classification of the varieties of *T. cacao*, removing Calabacillo from the Forastero group and making with it a third class, as follows:

Class I. Criollo or fine thin-skinned.

1. var. *a.* Amarillo
2. var. *b.* Colorado

Class II. Forastero or thick-skinned cacao.

3. var. *a.* Cundeamor verugosa amarillo.
4. var. *b.* Cundeamor verugosa colorado.
5. var. *c.* Ordinary amarillo.
6. var. *d.* Ordinary colorado.

7. var. *e.* Amelonado amarillo.

8. var. *f.* Amelonado colorado.

Class III. Calabacillo, or small-podded, thick, smooth-skinned, flat-beaned.

9. var. *a.* Amarillo.

10. var. *b.* Colorado.

Hart makes extensive and sound comments on the characteristics and qualities of each variety, saying, among other considerations, that "The finest cacao is by general consent admitted to be produced by the Criollo variety, and this is assumed to be identical or similar in character to that called the Caracas variety." (pag. 48). "The characteristics of the Criollo cacao are the thinness of its pod, its rounded beans and pale colour of the interior of the bean on section. The leaves of the tree are small when compared with the Forastero varieties, and the tree itself is not nearly so sturdy and thriving, and does not produce such regular and abundant crops as the Forastero and Calabacillo varieties. The skin of the bean itself is thinner, and the interior has but a small proportion of that bitter flavour which is characteristic of the unfermented bean of Forastero and especially that of Calabacillo. The flattest beans are those produced by pods of the Calabacillo type. The beans of Forastero are intermediate between these and the rounded form of the Criollo." (p. 51). Hart illustrates his important pioneer work with not too good illustrations of pods and its sections of Amelonado, Calabacillo, Forastero and Criollo, and with three diagrammatic sections of typical seeds of Criollo, Forastero and Calabacillo. He adds, however, that there will be found intermediate forms hardly reconcilable with any of the figures, so that "these are to be taken as representative only of the typical varieties with some latitude."

Hart's illustrations are not representative of the concepts for which the same nomenclature is generally used outside Trinidad: For instance, the figure given as Criollo represents the type Cundeamor, and the models he used to illustrate Calabacillo were not well selected. These facts explain the comments made some years later by Preuss about Hart's somewhat confusing nomenclatural concepts.

1898: John Donnell Smith describes a new *Theobroma* with yellow flowers and smooth cylindrical pods which Pittier and Tonduz discovered in the mountains of Costa Rica, *T. simiarum*.

1899: Jumelle publishes an excellent monographic compilation on cacao with a long chapter devoted to the botany following an interesting account of its history. Disregarding the work of Bernoulli, Jumelle follows Schumann in his treatment of the Sterculiaceae in the Flora Brasiliensis, declaring that "C'est certainement l'étude la plus complète et la plus consciencieuse qui ait été faite sur les *Theobroma*." Then he gives in French Schumann's complete key for seven

species. He recognizes that several species have been published before, based on weak characters, probably due to variations caused by cultivation or changes of soil or climate. Jumelle devotes much attention to the description of *T. cacao* and its different varieties. He follows in this the works, experiences, and classification of Hart. Chapters with descriptions and accounts are also devoted to *T. bicolor* (and separately *T. ovatifolium*), *T. angustifolium*, *T. subincanum*, *T. grandiflorum*, *T. speciosum*, *T. microcarpum*, and *T. glaucum*. Short notes are given to *T. sylvestre* Mart., *T. Martii* Schum., and *T. album* Bernoulli. Although excellent as a compilation, Jumelle's publication offers nothing original with regard to the systematics of *Theobroma*; its many illustrations were taken from Bernoulli, Schumann, and Hart.

1899: De Wildeman publishes a new binomial, *Theobroma Kalagua*, with a description and illustrations of leaves, flowers, and fruit. Unfortunately, this "new species" was based on separate elements belonging to different trees and different species from unknown localities, sent to de Wildeman by a Mr. Ch. Patin, at that time vice consul of Belgium in Panama. Although the specimens used for the description were claimed by Patin as having been collected from a single tree, Patin himself recognized later that they came from different trees and that the fruits were from *T. simiarum*. At that time, Panama was part of Colombia and that is the reason why the new species and the specimens were labeled as from Colombia.

1900: In a second work, Hart makes no alterations in his 1892 classification, stating that "after the lapse of some years I still see no necessity to revise the list." But he extended his comments on characteristics, variations, and properties of the cacao varieties with new considerations, as for instance: "Calabacillo is certainly as far removed from Forastero, as Forastero is from Criollo, as seen in plantations of the present day, when every intermediate form from Criollo down to Calabacillo can be seen linking the whole in one continuous chain of varieties. To properly classify Cacao, we must first know what the originals were like, and it is clear that at the present time, it is hard to decide exactly what were the forms assumed by the older types of Cacao fruit. There is an apparent consensus of opinion however which points to the thin-skinned and bottle-necked variety as the original Criollo (Spanish for Creole), and this is quite confirmed by the Criollo being discovered in the virgin forest of an uncultivated part of Trinidad" (p. 52).

The Criollo as well as the cacao of Java and Ceylon, the Criollo of Central America and *T. pentagonum* have the seeds white or almost white inside. The best quality Forasteros have the seeds slightly violet, and the Calabacillo strongly colored. He adds that the best

qualities of fruits of Venezuela (e.g., from Ocumare) are distinguished by the lightness of the seeds, and their shape, although the pod might belong to the type of Forastero. In Trinidad, in the Estates where certain strains of cacao from the continent had been introduced, we find the finest qualities of Forastero. The illustrations, with a similar nomenclature, are less clear than those of first edition.

1901: Paul Preuss publishes the first important field report ever written with keen observations on the varieties of cacao, conditions of cultivation, conditions and ways of preparation, and qualities of the products in several countries of South and Central America. It is the report of his trip made during 1899 and 1900, in order to obtain information on tropical crops for the Colonial-Economic Committee of the German government. From Surinam he names three varieties of *T. cacao* as cultivated: "Surinam," also called "Porcelaine" (corresponding to the Amelonado of Trinidad), "Aligator" (the Cundeamor of Venezuela and Trinidad), and "Caracas" (similar to Carupano or Forastero from Trinidad). He also observed mixed intermediate forms. From Trinidad and Grenada, where he saw extensive plantations, he describes several cultivars: "Amelonado," "Calabacillo," "Sangre de toro," "Forastero," "Criollo"; he mentions that Hart calls Criollo what is called Forastero in Venezuela and that Hart's Forastero is the Venezuelan Criollo. But according to Preuss, the formerly general use of the name Forastero in Trinidad applied to cacaos other than Criollo. At present, Forastero has the same meaning as Trinitario, which might have been introduced from the Venezuelan eastern coast or from the Orinoco region, after the earlier Trinidad plantations (all of the Criollo type) had been destroyed by some kind of disease. Preuss goes on to describe the three main Trinidad varieties using the concepts of Hart: "Forastero," "Amelonado," and "Calabacillo." He compares the yellowish variety of Amelonado to the Guayaquil cacao and the elongated form of Forastero to the Colombian cacao. Of Venezuela, Preuss says that it is the classic land of Criollo, producing large seeds with thin shell of the best quality. He distinguishes two main cacao varieties in Venezuela: 1) Cacao Criollo, 2) Cacao Trinitario. Preuss clearly distinguishes seven types, but there are also many intermediate forms.

1. Angoleta.
2. Cundeamor (Cundeamor legitimo, with red shell and Cundeamor amarillo, with yellow shell).
3. Carupano legitimo (Carupano grande, and Carupano mestizo, red with yellow).
4. Carupano parcho (yellow fruit).
5. Carupano Taparito (yellow or brownish).
6. Sambito (red or yellow, short, thick, rather smooth fruit).

7. Trinitario amargo or "Cojón de toro" (red or red brownish, smooth, blunt or shortly attenuate pointed fruit).

He describes the Criollo tree and mentions its three varieties: "Criollo legitimo" (the best quality) with deep red, "Criollo amarillo" with yellow, and "Criollo mestizo" with yellow and red shells. The seeds are white violet in the first and white in the second. Preuss sees in Ecuador a great uniformity in the cacao fruits as he had observed in no other country. They are of the Amelonado type, the same type being cultivated in the Cameroons, St. Thomé, Grenada, and Surinam; the Ecuadorian type has thicker shells. He mentions four varieties: "Arriba," "Balao," "Machala," and "Bahia." He says that cacao is frequent in the underlayer of the rain forests in Ecuador and that these wild trees, which cannot be distinguished from those of the plantations, also produce good fruits, which have very thick shells and roundish seeds in section. Preuss sees in this wild cacao the origin of the widespread plantations of the variety Amelonado (p. 247). *Theobroma bicolor* is also mentioned as a wild cacao ("cacao blanco," "bacao") in Ecuador.

From Central America he describes the native variety "Cacao Lagarto" (Alligator), the other native variety Criollo and two others introduced, the "Cauca" from Colombia, and "Trinitario" from Trinidad; in this Trinitario he distinguishes the three types Forastero, Amelonado and Calabacillo. There are intermediate forms between Lagarto and Criollo "Cacao del pais" difficult to separate one from another; they have red and yellow pods with a thin shell and white-violet or white cotyledons. The seeds of Nicaraguan Criollo are the largest of all varieties and of the best quality known. Mention is made and illustrations are given of *T. bicolor*, *T. angustifolium*, and *T. pentagonum* from Central America. Also drawings of fruits and seeds of five varieties of *T. cacao* (Nicaraguan and Venezuelan Criollo, Calabacillo, "Cundeamor Legitimo," and "Curupano grande") are reproduced.

1902: De Wildeman gives a taxonomic compilation of *Theobroma* in his book on tropical cultivated plants. Following Schumann he divides the genus in *Herrania*, *Eutheobroma*, and *Bubroma* and uses Schumann's key for the species (as in the Flora Brasiliensis), but adds another species, *T. simiarum* Donn. Smith, and accepts *T. pentagonum* as different from *T. cacao*; altogether, nine keyed species and four doubtful additional ones, as by Schumann, besides Herranias, are treated. For each species, summarized descriptions, native names and uses, geographic location, and miscellaneous comments, are given. Speaking of *T. simiarum* he writes: "Il faut rapporter en partie à cette espèce la plante que nous avons décrite, en 1899, sous le nom de *T. kalagua*, dont la description avait été fait sur de feuilles,

des fleurs et des fruits ne provenant pas de la même plante.” Some attention is given to *T. cacao* and the differences between its seeds and those of *Herrania mariaae*, based on anatomical sections and gross chemical analysis made by Heim. The varieties of *Theobroma cacao* are reduced to ten “series” distributed in three “grand” groups—I) Criollo with two varieties: 1) amarillo, 2) colorado; II) Forastero with varieties: 3) cundeamor verrugosa amarillo, 4) cundeamor verrugosa colorado, 5) amarillo, 6) colorado, 7) amelonado amarillo, 8) amelonado colorado; III) Calabacillo with varieties: 9) amarillo, and 10) colorado.

1904: Lignier, in a list of the Caen City Herbarium, mentions *Theobroma sativa*, as a Sagot collection from French Guiana without further comment on the author or synonym; it probably refers to *Cacao sativa* Aubl.

1904: Huber, a botanist at the Goeldi Museum, Belém do Pará, inaugurates a new epoch by publishing direct observations on the botany, ecology, and location of species of *Theobroma*. Huber found spontaneous and subsponaneous trees of *T. cacao* in several places of Amazonia and believes that it may really be indigenous in the forests of the Alto Purús Rio, Río Ucayali, and other places down to Santarém and Obidos.

1906: Huber extends his explanations on the indigenism of *T. cacao* on the alluvian soils of the Rio Alto Purús, in the inundatable forests around the mouth of Rio Acre, and along the rivers Ucayali, Japurá, Juruá, and Madeira. Among observations on other species (*T. microcarpum*, *T. speciosum*, *T. obovatum* (as *T. sylvestre*), *T. subincanum*, and *T. bicolor*) he shortly describes a new species from Peru, *Theobroma sinuosum* Pavon.

1906: Huber publishes a variety *coriaceum* of *T. speciosum* found in Brazil. At the same time, he mentions having found *T. cacao* growing wild in a forest near the Canchahuaya Lake.

1908: Chevalier, in his extensive studies on cacao crops in western Africa, besides detailed descriptions of the cocoa tree and its growth and ecology in Africa, mentions its variations and describes a new species, *Theobroma sphaerocarpa*, distinguished by its globose, almost smooth fruit 9 to 11 cm. in diameter, which has been cultivated for a long time on the island of São Tomé.

1911: Hart, in the introduction of his book on cacao, gives an excellent account of the varieties of the cultivated cacao, discussing the external features of the chief different types and the qualities of their crops:

“The species known as *Theobroma cacao*, covers innumerable varieties or forms, differing in shape of pods, in size and vitality of trees, in bearing capacity, and in colour, shape and quality of the bean.

The many names under which varieties of this tree (*Theobroma cacao*) are known, do not constitute species, but must be merely considered as varieties of one species. These varieties probably owe their origin to seed variation and cross-breeding, together with the local influence of soil and climate, but it would serve no useful purpose to record the names by which they are known, as these differ in each district, in each plantation, and in each country where they are grown" (p. 2).

"We have therefore a classification under *Theobroma cacao* carrying fourteen types under three classes, but it must be understood that these are separated by no definite margin, and that intermediate forms will be found on estates showing every conceivable form of variation" (p. 3).

Hart's classification here amplifies his initial one of 1892, mainly by broadening the concept of Criollo, in which class he includes types known under this name outside Trinidad a long time before.

THEOBROMA CACAO

Class I. Criollo

Trinidad Criollo.

- (1) Var. *a*. Amarillo=Yellow, thin-skinned, bottle-necked.
- (2) Var. *b*. Colorado=Red, thin-skinned, bottle-necked.

Venezuelan Criollo.

- (3) Var. *a*. Amarillo=Yellow, thick-skinned, high-shouldered, sometimes pointed.
- (4) Var. *b*. Colorado=Red, thick-skinned, high-shouldered, sometimes pointed.

Nicaraguan Criollo.

- (5) Var. *a*. Amarillo—Yellow
 - (6) Var. *b*. Colorado—Red
- } Thick-skinned, high-shouldered, and
very large beans with light-coloured
interior.

Class II. Forastero

- (7) Var. *a*. Cundeamor verugoso Amarillo=Yellow-warted.
- (8) Var. *b*. Cundeamor verugoso Colorado=Red-warted.
- (9) Var. *c*. Ordinary, or typical Amarillo=Yellow Forastero.
- (10) Var. *d*. Ordinary, or typical Colorado=Red Forastero.
- (11) Var. *e*. Amelonado Amarillo=Yellow, melon shaped.
- (12) Var. *f*. Amelonado Colorado=Red, melon shaped.

Class III. Calabacillo

- (13) Var. *a*. Amarillo=Yellow
 - (14) Var. *b*. Colorado=Red
- } Calabacillo, flat-beaned, smooth, thin-
or thick-skinned, and small pods.

THEOBROMA PENTAGONA

- (15) *Theobroma pentagona*=Alligator cacao. Has yellow, much-warted pods, with five distinctly raised ribs, and large beans, having white or light-coloured interior.

Hart characterizes the Criollo varieties by their light-colored seeds, the high quality of the cured product, and the less vigorous growth. The Forastero has light to dark purple seeds in large rough-ridged pods; it is rather variable and is a strong grower. Calabacillo is an inferior but stronger growing tree, having ovoid pods with thin, solid, dark-colored seeds. "*T. pentagona* has the largest seeds of any known species." "In general, however, it is hard to say where one form begins and another ends." In fact in most countries, cacao "consists of a heterogeneous mixture of cross-bred varieties of one species (*T. Cacao*) though of late years it is thought possible that the common species may have become hybridized with *T. pentagona*."

1914 and 1932: Van Hall publishes his well-known book on cacao which since then has been a textbook and main source of information for cacao growers and agronomists. In his botanical chapter he presents some nonoriginal information on the noncultivated *Theobromas*. He gives excellent comparative descriptions and evaluations of the most important variations and forms of cultivated cacao. He follows Morris in recognizing two groups: 1. Criollo; 2. Forastero. He describes seven types or subvarieties of the first: the Venezuelan, the Ceylonese, the Javan, the Samoan, the Madagascarian, the Nicaraguan, and the Surinam Criollos. The subvarieties of Forastero described are Angoleta, Cundeamor, Amelonado, and Calabacillo. *Theobroma sphaerocarpa* Chev. is considered a mere form of Calabacillo. In 1932, van Hall introduces a new name *T. aspera*, transferred from *Herrania*.

1914: Pittier publishes two new species of *Theobroma* from Panama: *T. bernouillii*¹ discovered by him in the forests of the Colon province, and *T. purpureum* which belongs to *Herrania*.

1915: Cook, after a thorough morphological field study of *T. bicolor* and *T. cacao*, especially of the branching system and the flower and inflorescence structure, decides that they belong to different genera, and publishes a new monotypic genus *Tribroma* with one species, *T. bicolor*; it mainly differs by its clusters of three branches and the woody pericarp in contrast to the 5-branching clusters and fleshy pericarp of *T. cacao*. Although all observations by Cook are very sound, he does not compare *T. bicolor* with other species of *Theobroma* besides *cacao*.

1916: Cook publishes in detail and with illustrations the results of his studies on growth and dimorphism of branches and leaves of *T. bicolor* and *T. cacao*. He explains the sympodial structure of the *Theobroma* stem, the verticillate primary branching, the formation and succession of upright lateral shoots, which continuing the main stem, bring the clusters into a lateral position and the alternate

¹ Originally so misspelled, although the correct name would have been "*bernouillii*."

branching of lateral branches. Cook describes the two types of leaves: the long petiolate symmetrical leaves of the seedlings and upright shoots and the bilateral, asymmetrical, dorsiventral, short-petiolate leaves of the lateral branches. The structure of inflorescences and flowers also are studied.

1918: Stahel publishes a precise, illustrated, morphological study of the structure of the inflorescences of *T. cacao* and *T. bicolor*. These inflorescences are always formed in the axil of the subtending bract of a lateral, non- or short-developing bud. The inflorescence in *T. cacao* consists of a cincinnous main axis with many short internodes and a few dichasial final branchlets. In *T. bicolor*, the main cincinnous axis has a few, long internodes, and the lateral branching is dichasial. The peduncles have a bilateral, the pedicels a radial structure.

1921: Benoist publishes a new species of *Theobroma* from French Guiana found by himself, *T. velutinum*. It is characterized by large leaves, velutinous beneath, and by ellipsoid, 5-ridged, velutinous pods.

1923: Standley recognizes three spontaneous species for the Mexican flora: *T. cacao*, *T. angustifolium*, and *T. bicolor*, and gives interesting historical, geographical, and economic data.

1925: Ducke publishes firsthand new botanical and ecological data on several Brazilian species.

1925: Pittier presents his interesting new theory that all existing forms of cultivated cacao are the result of hybridization between two initial species: 1) *Theobroma cacao* L., with elongate, claviform, rugose, 10-ridged pods, containing large, ovoid, white or slightly yellowish seeds, and 2) *T. leiocarpum* Bernoulli, with more or less rounded, smooth, slightly 5-ridged pods, with flattened, more or less triangular and dark purplish seeds. The first type is the one commonly known as "Cacao dulce" or "Cacao criollo," the second is commonly known as Calabacillo or Trinitario and in Guatemala as "Cumacaco." *T. sphaerocarpum* Chev. from São Tomé is a hybrid, retrogressive to *T. leiocarpum*. The two typical forms are united through an unlimited number of intermediate hybrid forms the characteristics of which are very variable; he says that the present nomenclature of varieties should be abandoned.

1925: Chevalier, in his "Observations" to the preceding work of Pittier, accepts basically Pittier's theory, and says that *T. sphaerocarpa* would be the extreme form of the series with smooth fruits and that *T. leiocarpa* is a hybrid between *T. cacao* and *T. sphaerocarpa*.

1926: Pittier answers Chevalier saying that he has never found *T. sphaerocarpum* in Central America, but that he has found growing wild in Costa Rica and Panama forms almost identical to *T. leiocarpum* Bernoulli. He recognizes that the forms with small, round pods often found in the region of Barlovento (Venezuela) are very close to *T.*

sphaerocarpum. Both original species are still found in pure, typical form and it can be said that in most plantations, next to the "primitive species" a number of hybrids are found. "We have still in Venezuela cacao plantations with absolute domination of the Criollo type, as, for instance, it happens at Caruao and Chuao." There can be observed over great extensions of land, tree after tree with elongated, claviform, pointed fruits, which may be reddish or yellow, with rounded seeds and almost white and insipid cotyledons. Pittier adds that at the time Linné described *T. cacao*, the Criollo was the dominant form in cultivation.

1930: Myers reports about his exploration of the upper Mamaboen Creek, a tributary of the Coppename River, where wild cacao was discovered by Stahel ten years earlier. This place is located in the middle of the Surinam rain forests, 40–50 kms. away from the last small Indian village. Abundant trees of cacao in a wild state were found in the lower tree-layer of the forest, under conditions of dense shade and high humidity; most of the cacao trees were found on the flooded margins of the river; few were found on higher ground. The trees were 10 to 25 feet high, and abundantly fruiting; the ripe pods were bright, light yellow in color, and almost smooth (with little indication of longitudinal ribs) and with 40 to 50 seeds with deep violet cotyledons. Myers adds that the fruits were of the Amelonado-Forastero type. He also comments on information about wild trees in other parts of Surinam, British Guiana, Brazil, and elsewhere.

1930: Pittier publishes an abridged key to classify the known species of *Theobroma*, including *Herrania*. Following Schumann in *Die Natürlichen Pflanzenfamilien* he divides it into three sections, the first being *Herrania*. The other two sections, defined by diantheriferous (Sect. *Eutheobroma*) and triantheriferous stamens (Sect. *Bubroma*), comprise 13 species, which are distributed in subsections corresponding to the Bernoulli sections. In *Eutheobroma* he includes subsect. *Cacao* with *T. cacao*, *T. leiocarpum*, and *T. pentagonum* and subsect. *Rhytidocarpus* with *T. bicolor* and *T. Bernouillii*. In *Bubroma* there are subsect. *Telmatocarpus* with only *T. microcarpum*, subsect. *Oreanthes* with *T. spruceanum*, *T. speciosum*, and *T. simiarum* and subsect. *Glossopetalum* with *T. angustifolium*, *T. grandiflorum*, *T. subincanum*, and *T. sylvestre*. The characters given in the key are few and not always the most typical or correct, some of the species being wrongly placed (*T. Bernouillii*, *T. simiarum*). The binomials *T. glaucum*, *T. martii* and *T. album* are considered dubious. Pittier refers to having received from Cook photographs of two forms of cacao cultivated in Peru with small fruits which might be different species; one has almost spherical, rugose pods called locally "cacao chuncho." Pittier says that, with the exception of *T. leiocarpum* and *T. cacao*

(respectively Calabacillo and Criollo), there do not exist stable forms of cultivated cacao. Forastero from Trinidad stands between these original species and can be considered as the result of their crossing. The Trinidad Forastero seems to be quite different from Venezuelan and Central American Forastero and probably from the Old World Forastero. He also says that it does not make sense to talk about the origin of Forastero, because its forms appear wherever the parental species are present and successive crossings produce constant variations. Commenting on the finding of Myers in Surinam, Pittier says that the wild cacao of the Mamaboen valley belongs to *T. leiocarpum*. The same opinion is expressed in connection with Schomburgk's spontaneous cacao found in the Río Branco valley and numerous references about wild cacao throughout the Venezuelan Guayana. The cacao with tapering, pointed, ridged and rugose pods with white cotyledons (*T. cacao*) has really never been found indigenous to the east of the Panama isthmus. Pittier found it at the isthmus but says that the origin of this species is to be sought towards the north, in the Soconuzco, Chiapas, and Tabasco regions, where the Criollo type finds the best conditions for its development. Conversely, the plantations of Calabacillo do not go much further west than Costa Rica where it was recently introduced. Here are to be found the westernmost stations of *T. leiocarpum*, although the type came from plantations in Guatemala.

1931: Mildbraed publishes a new species *T. tessmannii*, found by Tessmann in eastern Peru. He relates it to *T. ferrugineum* Bernoulli, from which it differs especially by the long, soft tomentum of the leaves beneath.

1932: Cheesman, who had been conducting research on cacao corps for many years, presents a significant account of the economic botany of *Theobroma*. He believes that it is unlikely that any of the now uncultivated species has any direct economic significance. He speaks about the cultivated species, those of section *Cacao*, as interfertile species (*T. cacao*, *T. leiocarpum*, *T. pentagonum*). Cheesman says that "the taxonomic status of the group of forms at present included under the collective term *T. cacao* can only be determined by prolonged research, including genetic, and possibly also cytological studies." Cheesman agrees with Pittier in considering that more than one species contributed to build the "cacao complex," adding that this idea provides the most helpful way of regarding the extraordinary variation exhibited by the crop. His discussion on the history, characters, and merits of the varieties is illuminating in many respects, especially when trying to understand their possible origin. In practice, he follows, with slight modification, van Hall's classifica-

tion which he says "is a compromise between a natural and an artificial system."

1932: Pittier insists in his viewpoints on the origin of the cultivated cacao. Finding that *T. cacao* L. is not well typified by a known variety, Pittier decides to abandon this name and to substitute for it *T. sapidum*, but no specific description is given and a type specimen is not indicated. The Calabacillo seems to have a stronger fertilizing power than the Criollo which explains why few trees of the first suffice to alter the plantations of the second.

1933: Ciferri makes a very detailed, critical study of the cultivated cacaos of Santo Domingo giving a thorough classification with definition, descriptions, and illustrations of their numerous types. Morphological, taxonomic, historical, and economic comments are given. Ciferri follows the principles of Pittier in accepting the theory that the majority of the cultivated cacaos are hybrids of two initial types, but he considers these two types varieties instead of species. Ciferri gives the system formal nomenclatural status by publishing the following new varieties: *T. cacao* L. *emend.* var. *typica* Ciferri; *T. cacao* L. *emend.* var. *leiocarpa* (Bernoulli) Ciferri, and *T. cacao* var. *typica* × *T. cacao* var. *leiocarpa* = Forasteros. "I cacao denominati globalmente "Forasteros" sarabbero dunque, secondo l'idea di Pittier, che moi adottiano in pleno, i meticci tra le due varietà sunnominate del *T. cacao*." Ciferri's work is a significant contribution to the knowledge of cacao varieties and their distribution.

1935: Cheesman describes the branching system and dimorphism in cacao, and studies different ways of vegetative propagation.

1936: Campos Porto publishes information on the species of *Theobroma* cultivated at the botanical garden of Rio de Janeiro, with a photograph of the inflorescences of *T. speciosum*; the other species referred to are *T. cacao*, *T. bicolor*, *T. grandiflorum*, *T. subincanum*, and *T. microcarpum*.

1937: Standley lists and describes five species of *Theobroma* in his Flora of Costa Rica plus a *Herrania* as *T. purpureum*. He considers *T. simiarum*, *T. angustifolium*, *T. bicolor*, and *T. cacao* to be wild in the forests and *T. leiocarpum* as probably wild.

1937: Pérez Arbélaez publishes a manual for the cacao growers of Venezuela including a botanical introduction with descriptions of and information on Venezuelan cultivars; he also gives interesting historical data.

1938: Pound finds interesting varieties of cacao in his explorations in South America, especially in the upper Amazon basin.

1938: Bondar publishes a documented book on the cultivation of cacao in Bahia. He gives comments and a key to the known species of *Theobroma*. He considers that the varieties cultivated in Bahia for

many years belong to *T. leiocarpum*; a great uniformity in the product exists, but he believes that recent introductions of Criollo may well stop this uniformity. He also describes and illustrates several forms of Forasteros known in the region.

1939: Diels publishes a new species, *T. calodesmis*, found by Hertha Schultze-Rhonhof in the rain forests of eastern Ecuador, which he relates to *T. speciosum* and *T. bernouillii*.

1939: Cope's investigations in Trinidad on agents of pollination using thrips (*Frankliniella parvula* Hood), red ants (*Wasmannia auropunctata* Rog.), and aphids (*Toxoptera aurantii* B. de Fousc.), suggests that red ants and thrips are the responsible agents of pollination in a cacao population at River Estate.

1940: E. W. Emmart publishes the Badianus Manuscript, the earliest book ever written on Mexican medicinal plants, the work of two Aztec Indians, Martinus de la Cruz who composed the work in Aztec, and Juannes Badianus who translated the text into Latin. On plate 68, illustrating six plants, plant no. 2 represents "Tlapalcacauatl," colored cacao, i.e., "tlapal" = colored, "cacauatl" = cacao, according to Emmart (p. 273), who adds, "This picture is the earliest illustration of the cacao, *Theobroma cacao* L., the source of chocolate." This interesting, primitive drawing clearly illustrates the Criollo variety.

1940: Ducke summarizes his experience of many years in Brazilian cacaos with a new and detailed key to the Brazilian species. He brings new data into consideration in his classification, as for example fruit characters that were unknown before. He gives photographic illustrations and new information, based on direct field observations, about morphological, phenological, and ecological features of the species treated, which are *T. cacao*, *speciosum*, *spruceanum*, *microcarpum*, *obovatum*, *subincanum*, and *grandiflorum*. He also includes in *Theobroma* the genus *Herrania* with one species, *T. Mariae*. Concerning *T. cacao*, Ducke recognizes it as indigenous throughout the central and western Amazonia. Ducke considers *T. leiocarpum* Bernoulli a mere form of *T. cacao* and makes the new nomenclatural combination: *T. cacao* L. forma *leiocarpum*.

1942: Schery publishes a new species, *T. asclepiadiflorum*, based on specimens from Panama.

1944: Cuatrecasas publishes a new species with yellow flowers, *T. cirmolinae*, found by the author in the rain forests of the western slopes of the western Andes in Colombia.

1944: Cheesman makes a thorough examination of the taxonomic situation in cacao, the most important conclusion being that the whole assemblage of wild, semiwild, and cultivated cacao constitutes "one interbreeding population." He still supports the main division of

cacao into two groups of varieties, Criollo and Forastero. He proposes the new theory that the Criollo, which may occur wild in some regions from southern Colombia to southern Mexico, may have originated at the headwaters of the Amazon. He divides this group into Central American and South American Criollos. The Forasteros are divided into Amazonian Forasteros, which can be found wild in Amazonia and which are widespread in cultivation, and the Trinitarios, possibly originating from the mingling of South American Criollo and Amazonian Forastero stocks. *Theobroma pentagonum* is a simple form of *T. cacao*, probably a segregate of the large cross-fertilized population. The same opinion is expressed with regard to *T. leiocarpum*, which, according to Cheesman, does not belong to Amelonado; it is an aberrant form of the Criollo, for which reason the binomial falls into the strict synonymy of *T. cacao*. The data assembled and arguments of Cheesman are a very valuable contribution.

1946: Chevalier publishes a monographic revision of *Theobroma*. He recognizes 13 species (excluding *Herrania*) arranged according to the five sections of Bernoulli. He includes in the first section (*Cacao*) only *T. cacao*, in section II, *Oreanthes*: *T. guianensis* and *T. spruceana*; in section III, *Rhytidocarpus*: *T. bicolor*, *T. glauca*, and *T. Bernouillii*; in section IV, *Telmatocarpus* only *T. microcarpa* and in section V, *Glossopetalum*: *T. sylvestris*, *T. obovata*, *T. ferruginea*, *T. grandiflora*, *T. angustifolia*, and *T. simiarum*. In the key (Tableau Analytique), the species are differently arranged; they are divided in the two sections of Schumann: *Eutheobroma* with four species (*T. cacao*, *T. bicolor*, *T. Bernouillii*, and *T. glauca*), and *Bubroma* with the other nine species. The characters given in the key are not always well chosen, and some species are misplaced in the sections (as, e.g., *T. glauca* and *Bernouillii*). The nomenclature and typification of the species are not always correct; the concepts of *T. speciosa* Willd. ex Spreng., *T. guianensis* (Aubl.) Gmel., *T. velutina* Benoist, *T. sylvestris* Mart., *T. sylvestris* (Aubl.) Don., *T. obovata* Klotzsch ex Bernoulli, *T. ferruginea* Bernoulli, *T. sinuosum* Pavón and others are actually not clarified. Some confusion is also brought with the new names *T. sagittata* Pavón, *T. hastata*, and *T. undulata*. I have identified *T. sagittata* Pavón as *Herrania nitida* and suppose that *T. hastata* Cheval. is a *lapsus calami* for the former and *T. undulata* Cheval. a *lapsus calami* for *T. sinuosum*.

Special treatment is devoted to *T. cacao*, with which Chevalier had long and sound experience. He considers all cultivated cacaos as belonging to a single species, *T. cacao* L., in which four different races or "species jordaniennes" can be recognized. These races, which cross among themselves "à l'infini," can be only distinguished by their

fruits and seeds. These are lacking in herbaria, and therefore the races must be studied in the field. Four of the races or Jordanian species of Chevalier correspond to formerly described species (*T. sativa*, *T. leiocarpa*, *T. pentagona*, and *T. sphaerocarpa*) but he adds a fifth based only on foliage, *T. sagittata*, which, as I have pointed out, is not a *Theobroma*. Chevalier's classification for the "formes jordaniennes" of *T. cacao* L. follows:

Leaves obovate-oblong, acuminate.

Fruits ovoid-oblong 5-10 ridged, \pm rugose-bullate, long-attenuate into a point *T. sativa*

Fresh seeds yellowish white var. *leucosperma*

Fresh seeds dark violet var. *melanosperma*

Fruits ovoid, rounded at apex, smooth or with 5-10 shallow furrows . *T. leiocarpa*

Fruits globose, more or less smooth, rounded or depressed at apex . *T. sphaerocarpa*

Fruits ovoid-oblong narrowed to the apex, with 5 very prominent ridges. *T. pentagona*

Leaves narrowly oblong, or oblong-acuminate, more or less undulate . *T. sagittata*

Chevalier goes on to describe the three first "races," and declares that he had insufficient information on the other two. Chevalier uses for what he calls races, Jordanian species, or Jordanian forms, the same binomial denomination as for species, for instance, *T. cacao* L. forma *T. sativa* which should be *T. cacao* L. forma *cacao* according to the present rules of nomenclature. It seems right to consider the original species described by Linnaeus as belonging to the Criollo form, but nothing is clarified by Chevalier using the binomial *T. sativa*, because this name was based on *T. cacao* L. Chevalier considers his *T. sativa* originally from Central America. To the "Jordanian form" *T. leiocarpa* Bernoulli, Chevalier refers the "Cacao creoulo" of São Tomé, the Cumacaco, Calabacillo, and Trinitario, and he supposes it originated in Guiana and Brazil. Concerning the Jordanon *T. sphaerocarpa* Chevalier, described on São Tomé (Africa) plants, very similar specimens have been found in Venezuela (var. *sambito*), in the high Amazonian forests, and at the Rio Marañón. The Jordanon *T. pentagona* has never been found wild; it seems to be originally from Central America. The experience and opinions of Chevalier have to be taken into account when considering the classification and origin of cultivated cacaos.

1946: Cuatrecasas publishes *T. capilliferum* discovered on the Pacific coast of Colombia.

1947: Llano Gómez publishes information about the cultivated cacao in Colombia, with several plates in color representing the principal types.

1948: Rombouts discusses *Theobroma Saltzmaniana* Bernoulli, showing that it might be based on a flower with defective or abnormal

petals and therefore cannot be distinguished from other forms of *T. cacao*.

1949: Standley and Steyermark consider five species of *Theobroma* in their Flora of Guatemala, recognizing *T. pentagonum* and *T. leiocarpum* as different from *T. cacao* following Bernoulli. *T. angustifolium* is given as cultivated and *T. bicolor* as uncertainly native.

1949: Cuatrecasas and León describe a new species, *T. mammosum*, collected by León as a rarity on the Atlantic coast of Costa Rica.

1950: Holdridge publishes some new information on Mexican and Central American species of *Theobroma*, with a key to nine species and one *Herrania*. He suggests that *T. pentagonum* might be the original type and source of the cultivated cacao in Mexico and Central America and that the Criollo types were the product of interbreeding of *T. pentagonum* with the South American *T. leiocarpum*.

1950–1953: Cuatrecasas publishes *T. stipulatum* and *T. nemorale* from the rain forests of the Pacific coast of Colombia and *T. gileri* from the Pacific range of Ecuador.

1951: Freytag publishes a revision of *Guazuma*, which helps in the study of its relationships of *Theobroma*. The genus is reduced to four species.

1951: Addison and Miranda Tavares explain the results of their six-year work in trying to produce hybrids from different *Theobroma* species. They crossed *T. cacao* with all the Amazonian species of *Theobroma*, without success, and proceeded then to cross the other Amazonian species. In 1946, from 719 pollinations of *T. speciosum* on *T. cacao*, they obtained 29 fruits and 979 seeds, which were mostly abnormal and did not germinate. Same results were attained by a few pollinations with *Herrania mariae*. Among 798 cases of pollination of *T. microcarpum* on *T. cacao* 11 fruits and 26 seeds were produced, from which only three seedlings were produced which grew no more than 10 cm. Similar negative results were produced from *T. cacao* \times *obovatum* and *T. bicolor* \times *cacao*. Some particular trees of *T. cacao* were more receptive than others; one of them gave fruits when submitted to pollination from all other species. When *T. cacao* was used as pollinator on *T. microcarpum*, *T. speciosum*, and *H. mariae*, no fruits or seeds were obtained. In 1947, another series of cross-pollinations were made on *T. cacao* with similar results, although a few more or less viable hybrids were produced, e.g., *T. cacao* \times *microcarpum* gave 28% fruits, but these decayed after developing one month.

Better results were attained by Addison and Miranda in crossing *T. grandiflorum* and *T. obovatum*; many hybrid seedlings were produced and several developed into perfect trees (in 1½ years); the leaves, fruits, and flowers of the hybrids showed intermediate char-

acters, and the pollen grains were normal and fertile. Well-developed hybrids between *T. grandiflorum* and *T. subincanum*, *T. obovatum* and *subincanum*, and *T. speciosum* and *T. sylvestre* (= *spruceanum*) were also produced. In 1948, some fruits were obtained by crossing *T. cacao* with *T. grandiflorum*, but these gave very few seeds, from which only few plants developed up to 15 cm.

Addison and Miranda also made grafting experiments with good results using *T. grandiflorum*, *T. obovatum* and *T. subincanum*. *T. bicolor*, *T. speciosum* and *T. sylvestre* (*spruceanum*) proved to be another successful grafting group.

During their experiments, Addison & Miranda had the opportunity of making interesting morphological and physiological observations. The seeds of *Theobroma* usually germinate within 15 days. *Theobroma subincanum*, *obovatum*, *grandiflorum*, *microcarpum*, and *H. mariae* were found to have hypogeous germination, whereas *T. cacao*, *sylvestre* (*spruceanum*), *bicolor*, and *speciosum* have it epigeous. The very young leaves are green in *T. speciosum*, *sylvestre*, *bicolor*, and *microcarpum*, but they may be green or red in the other species.

1952-1953: The Anglo-Colombian Cacao-Collecting Expedition publishes reports on its explorations in the search for wild and cultivated species of *Theobroma* and *Herrania* in Colombia. The expedition took place from June 1952 to October 1953, with the participation of the British botanists and specialists F. W. Cope, D. J. Taylor, R. E. D. Baker, P. C. Holliday, and B. G. Bartley. The Colombian botanists who joined the expedition were H. Garcia Barriga, Canuto Cardona, R. Romero Castañeda, and Alvaro Fernandez P. The main areas explored were: (1) parts of the rivers Caquetá, Apaporis, Vaupés, Negro (Guainía), Inírida, and their tributaries in the provinces of Amazonas and Vaupés, from 1°30' S. to 3° N. and from 67° W. to 71° W.; (2) parts of the rivers Putumayo, Caquetá, and Caguán in the provinces of Caquetá and Putumayo, from 0°20' S. to 2° N. and from 74° W. to 77° W.; (3) parts of the trans-Andean provinces of Valle del Cauca and El Chocó, from 3° N. to 6° N. and between 76° W. and 78° W.; (4) scattered areas in the provinces of Antioquia, Norte de Santander, Magdalena, Santander, and Huila.

The expedition made 191 botanical collections, of which 63 were of living material sent to Trinidad. The well-preserved specimens have been extremely useful for the study of the species and their geographical distribution. Twelve indigenous species of *Theobroma* were collected (*T. calodesmis*, *microcarpum*, *subincanum*, *grandiflorum*, *obovatum*, *capilliferum*, *gileri*, *nemorale*, *cirmolinae*, *simiarum*, *stipulatum*, and *chocoense*). *T. bicolor*, always found planted, and *T. cacao* were also collected. In a very few areas (Río Caguán, Río San Miguel) spontaneous trees of cacao were found inside the forest but under

circumstances that make it impossible to say with complete certainty that these trees were spontaneous. In general the subsponaneous and planted cacaos found in the southeastern region of Colombia were of the very uniform Amelonado type. The information and materials (living and preserved) gathered by this expedition are a very important contribution to the knowledge of *Theobroma*.

1954: Ducke makes a revision of his previous synopsis of the Brazilian species, incorporating new morphological data into an accurate, precise, well-balanced key. He introduces the character of the ramification being 5-whorled and 3-whorled in separating *T. cacao* from the other seven Brazilian species (*T. bicolor*, *T. speciosum*, *T. spruceanum*, *T. microcarpum*, *T. obovatum*, *T. subincanum*, and *T. grandiflorum*). Ducke considers each fertile stamen as the union of two or three (stamens geminous and trigeminous), and as Addison, Molina, and Pires had already observed before, characterizes *T. spruceanum* as having geminous stamens. Ducke still retains *Herrania* in *Theobroma*, with two Brazilian species, *T. Mariae* and *T. Camargoanum* (Schultes) Ducke. He summarizes the ecology and distribution of the genus in Brazil, calling it a typical Amazonian genus; he writes that it is not absent in any place in Amazonia where rain forest exists.

1956: Cuatrecasas recognizes seven species of *Theobroma* for the Flora of Peru: *T. calodesmis*, *T. grandiflorum* (planted), *T. obovatum*, *T. speciosum*, *T. subincanum*, *T. bicolor*, and *T. cacao* subsp. *leiocarpum*, which is found spontaneous in the rain forests of Peru.

1958: Schultes publishes the results of his discoveries and research on *Herrania*. His synopsis comprises 17 species, eight of them new. One species spreads northwards to Costa Rica, and the others are limited to the humid tropics of South America. This monograph shows the consistent unity of the group *Herrania* and the consistency of the characters that may be used to separate it from *Theobroma* and other related genera.

1958: Mora Urpi found a much greater variability in *T. cacao* throughout Mexico and Central America than in South America. In Central America and southern Mexico there can be found today practically all the known forms of cacao, for which reason Mora believes that Central America has been the center of domestication of the cultivated cacao; historical data also support this theory. He considers cacao as having been probably introduced in South America in pre-Colombian times. The geographical distribution of the Criollo type would also prove this theory. The author agrees with Holdridge in considering the *pentagonum* form as playing an important role in the origin of the cultivated hybrid complex; he considers *pentagonum* native in Central America and the original and most ancient form

of *T. cacao*, from which, through mutation, introgressive hybridization, and geographical isolation, the present population arose (p. 34).

1959: Soria confirms the observations of Mora about the great variation in the characteristics of shells and seeds of *Theobroma cacao* in plantations in Nicaragua. Trying to establish the correlation between pod shape and color of the seeds, he found that dark-colored seeds occurred in a large percentage of Criollo type pods, and white seeds were often found in pods of the Forastero and Calabacillo types. This agrees with the previous observation by Mora of dark seeds in the *T. pentagonum* pod-type. These observations, according to Soria, show that it is probable that the genetic factors controlling these characters are independent of each other. Soria sees as reasonable Holdridge's theory that Criollo cacao is a result of crosses between *T. pentagonum* and *T. leiocarpum*. But he adds "The possibility cannot be overlooked, however, that the Criollos originated as mutations in populations on the periphery of the area of distribution of the species, the mutations afterwards being fixed and maintained through geographic isolation and selection. In this case, *pentagona* could be a product of mutations in Criollo cacaos." Soria emphasizes that *pentagonum* can be fertilized very easily in either direction by other types of *T. cacao*. Mora observed such hybrids as often having conspicuous characteristics of *pentagonum*. "All these observations lead to the conclusion that *pentagona* is nothing more than one of the extremes in the variability of the complex of types forming the species *T. cacao*."

1960: At the River Estate Experiment Station of the Imperial College of Tropical Agriculture in Trinidad, 13 species of *Theobroma* were planted for research and observation. Cope and Bartley suggest the possible interrelationships of species of *Theobroma*, distributing them in two groups: 1) with epigeal germination and growth continuing from below jorquette, comprising *T. cacao* with 3-5-branched jorquette and *T. bicolor*, *speciosum* and *calodesmis* with 3-branched jorquette; 2) hypogeal germination and growth continuing from above jorquette in *T. microcarpum*, *grandiflorum*, *subincanum*, *obovatum*, *angustifolium*, *mammosum*, *simiarum*, *cirmolinae*, and *nemorale*. This is the first attempt to classify the genus on the basis of germination and branching.

1960: Cristóbal publishes an excellent monograph on *Ayenia* with important information concerning the relationships with other genera of Sterculiaceae.

1960: León, in Hardy's Cacao Manual, summarizes the taxonomy of *Theobroma*, recognizing 19 species and considering as doubtful *T. kalagua*, *tessmannii*, *ferruginea*, and *glauca*. He gives abridged descriptions and distribution for *T. cacao*, *bicolor*, *bernouillii*, *capillifera*,

calodesmis, *asclepiadiflorum*, *microcarpa*, *gileri*, *guianensis* (= *speciosa* sensu Chevalier), *spruceana*, *angustifolia*, *cirmolinae*, *grandiflora*, *mammosa*, *obovata*, *simiarum*, *stipulata*, *sylvestris* (= *subincana* sensu Chevalier), and *nemoralis*. The fruits of 17 species are illustrated. In the classification he follows more or less Chevalier; under *T. cacao* he distinguishes three subspecies: *sativa* (Lam.), *leiocarpa* Bern. and *pentagona* (Bern.); the listed cultivars are classified according to van Hall.

1961: Soria reports on cacao in Mexico, having visited extensive plantations in Tabasco. Before 1900, the variety cultivated in Mexico was almost exclusively Criollo, but at present that is disappearing, hardier and more productive varieties being substituted. He observes great variability in the pod form in plantations of old Criollo, which always have white seeds. Great variation is also seen at present in the widespread hybrid populations that resemble the Trinitario of South America, although the Mexican types lack the red pigmentation of the shells usually exhibited by Trinitario. (They are mostly whitish green or slightly reddish.)

Morphology

STEM AND BRANCHING (Fig. 1).—There is a dimorphism in the vegetative organs of *Theobroma*. The main stem and the adventitious orthotropic shoots have a radial structure, and the normal, plagiotropic branches are monopodial and dorsiventral. The trunk is sympodial.

The seedlings have an erect stem with regular, long-petiolate leaves arranged in phyllotaxy cycles of 5/13, 5/8, or 3/8 (Cook, Baker). After reaching a height of a few feet the vegetative end of the stem stops growing and by the way of a cluster of secondary buds it forks into 3 to 5 spreading branches arranged in a terminal whorl called a "jorquette" or "fan." These branches are plagiotropic and dorsiventral, with alternate, distichous, short-petiolate leaves with a phyllotaxy of 1/2. Further growth of the stem may now take place by two different ways: 1. One of the dormant buds axillary to the branches of the jorquette, and therefore adjacent to the central, inert, apex of the stem, develops into a new vertical shoot with the same structure as the main stem and looking like its continuation. It grows to a limited extent, ending also with a whorl of 3 to 5 branches; from above this second whorl or jorquette a third shoot is developed in the same way, forming a third internode of the stem, and so on. By this way a sympodial main trunk is built, with alternating internodes and nodes with regularly centered verticils of branches. Since new terminal shoots are produced above the jorquette next to the

apex we can call this pseudapical growth. 2. No buds at all develop above the first whorl of branches but an adventitious lateral one below it grows into a vigorous upright shoot with a structure similar to that of the main stem. Although lateral, it forces the node of the jorquette to one side, and takes progressively the central position of the stem, of which it will appear to be the continuation. After reaching some length it forks, ending in a jorquette; a new adventitious shoot is formed below that jorquette and so successively a sympodial trunk is built, with alternating internodes and irregular nodes. In this case the trunk is usually not truly straight and the whorls of branches, in spite of the fact that these tend to take a circular position around the stem, are always more inclined to one side, often making a lateral bunch; the closer to the jorquette the lateral adventitious shoots originate, the less irregular is the appearance of the sympodium resulting. We can call this subterminal growth.

The dimorphism of the stems is transmitted by the buds. Those of the seedlings and upright (orthotropic) shoots produce only, again, orthotropic shoots (chupons) bearing long-petiolate leaves and producing only the plagiotropic, dorsiventral branches of one terminal jorquette. The buds of the lateral, plagiotropic branches produce only other plagiotropic branches. Only exceptionally due to special physiological conditions or following mechanical injuries (e.g., trimming), do plagiotropic branches originate upright shoots (chupons). More exceptionally the extraordinary formation of alternate plagiotropic branches has been observed on upright stems which have failed to form a jorquette (Baker 1961, p. 9), but this has to be considered an abnormal case due to unknown special conditions of some cultivated trees.

The lateral, plagiotropic branches are monopodial and branch by axillary buds; frequently the growth of a lateral branch bends the young joint of the primary branch forcing this into an angle, thus simulating a dichotomous fork; branches may appear several times forked and are then called "dichotomous" branches.

The stem and branching dimorphism is important in the practice of propagation and cultivation of *Theobroma* trees, because only the trees produced by cuttings of orthotropic stems (chupons) are upright and regular; conversely, those from plagiotropic (dorsiventral) lateral branches, branch bilaterally (dorsiventrally) and tend to slant or to bow (incline), being thus weaker. In cultivated cocoa the formation of adventitious upright shoots (chupons) on branches and at the base of the trees is frequently observed; they may be used in practice to regenerate old trees by pruning, and as cuttings for propagation. But the production of chupons is always too small to serve for ex-

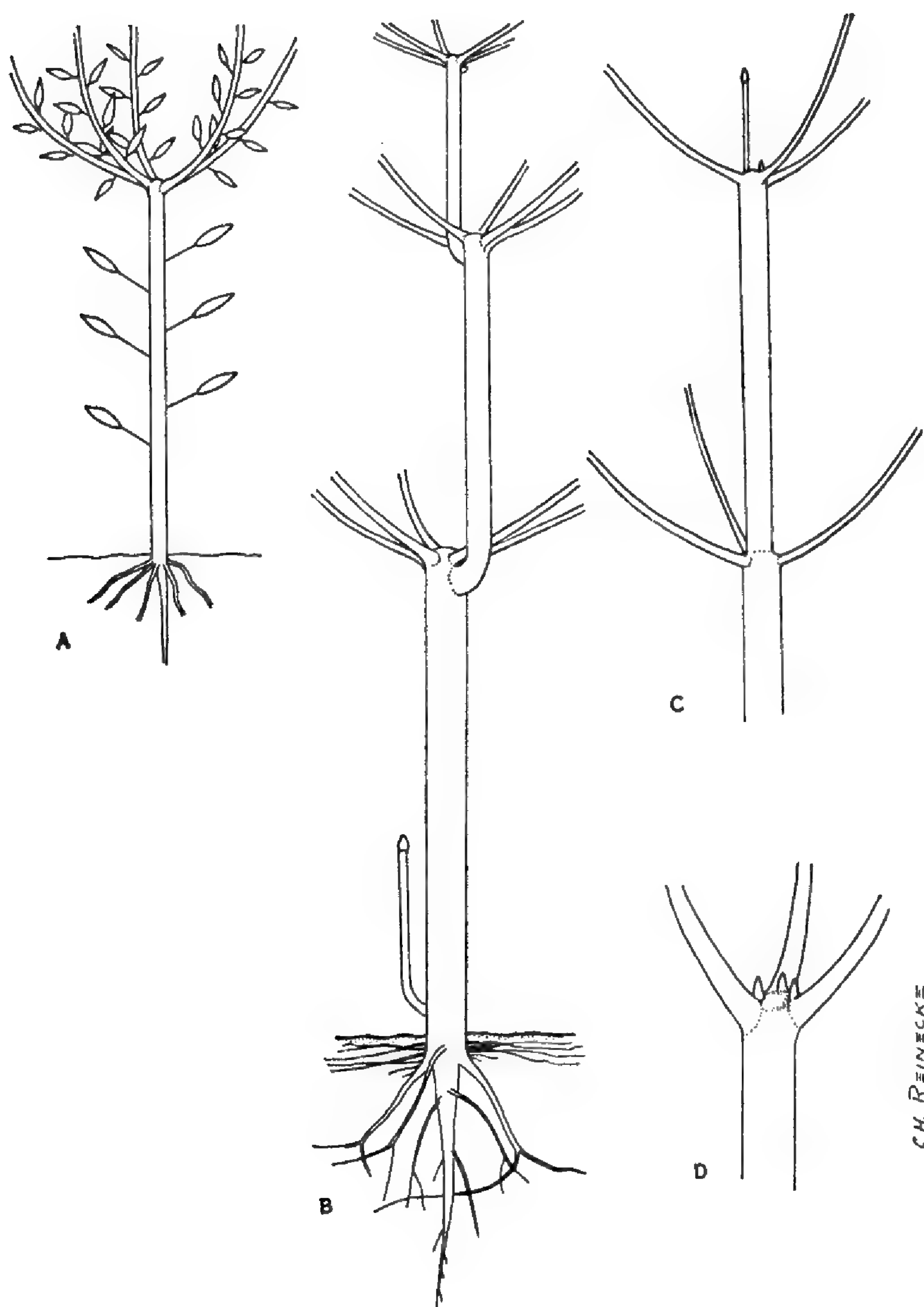


FIGURE 1.—Stem growth in *Theobroma* trees. A, B, subterminal or subapical growth: A, adult seedling of *T. cacao* with its primary stem (bearing long-petiolated, radially arranged leaves) topped by a whorl of dorsiventral, leafy branches; B, formation of the sympodial trunk in *T. cacao* by way of upright adventitious shoots from buds borne below the terminal verticil (or jorquette). C, D, pseudoterminal growth: C, formation of the sympodial trunk by developing one of the axillary buds of the terminal whorl of branches (e.g., sect. *Glossopetalum*); D, apex of stem topped by a whorl of 3 branches each with an axillary bud, of which only one will develop (growth above jorquette).

tensive propagation. The two different kinds of stem growth have taxonomic implications.

LEAVES.—There is a dimorphism of leaves correlated with the dimorphic stems. The leaves are arranged in several phyllotaxic cycles ($5/13$, $5/8$, $3/8$ have been recorded) around the radial, orthotropic stems or shoots, and are distichally alternate ($1/2$ phyllotaxy) on plagiotropic (lateral) branches.

The first leaves (on orthotropic stems) are long-petiolate and symmetrical. The petiole is elongate and thickened at both ends, forming a long, cylindrical pulvinus below the lamina and a more tubercular, shorter one at the base; this normal type of petiole facilitates all kinds of orientation to the blade.

The leaves of plagiotropic branches (the normal ones of the mature tree) are short-petiolate and asymmetrical. The petiole is with very few exceptions reduced to the thickened part of the cushions. The blade has more or less markedly unequal halves, especially at the base, which may be extremely asymmetrical.

The blades are simple and pinnatinerved, thick-coriaceous or chartaceous, with a strong midrib and several alternate, spreading-ascending, prominent secondary nerves; there are elevated tertiary nerves. Lesser ones form a small usually conspicuous reticulum. Often the lowest pair of secondary nerves is somewhat more separated from the next pair than the others, and may give some impression of a trinerved base; sometimes there are one or two stronger developed tertiary nerves, giving some appearance of a 5-nerved or 7-nerved base, but usually the main costa is much stronger than the secondary nerves and these are thicker than the tertiary, so that the mainly pinnate arrangement is always clear. In some cases, as in the primary leaves of *T. bicolor*, the lateral lower nerves are more clearly arranged so as to show a 5–7-nerved base, and some botanists describe them as palmatinerved.

The shape of the blades is often ovate, obovate-elliptic-oblong, or lanceolate, and usually acuminate at apex and obtuse or rounded at base, but there is a great deal of variation from one species to another. The margin is basically entire, but sometimes slightly sinuate or broadly dentate in adult leaves; the primary leaves may be coarsely dentate in the upper half. Indument is present except in a few species; most species have a more or less dense tomentum on the underside, which may be composed of one, two, or three different kinds or sizes of stellate hairs. This tomentum may cover the whole lower surface of the leaves entirely or may cover the areoles between the reticulum leaving all or part of the venation glabrous. The different kinds of hairs and their distribution supply good taxonomic characters.

INFLORESCENCE (Fig. 2).—The inflorescence is of the definite type. In some cases it may be a well-branched dichasium as in *T. bicolor*, but generally, the dichasium is totally or partly reduced to a monochasium

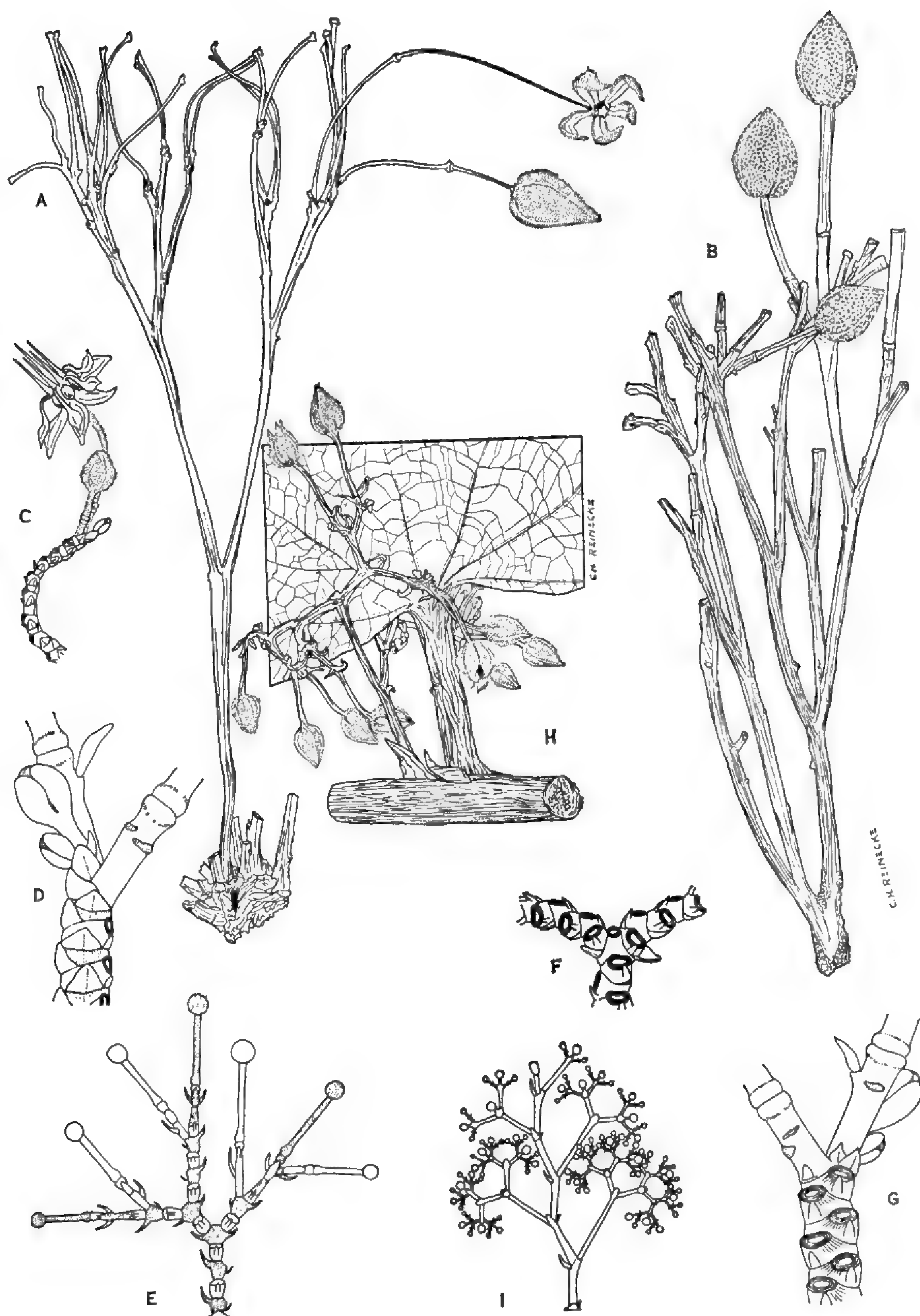
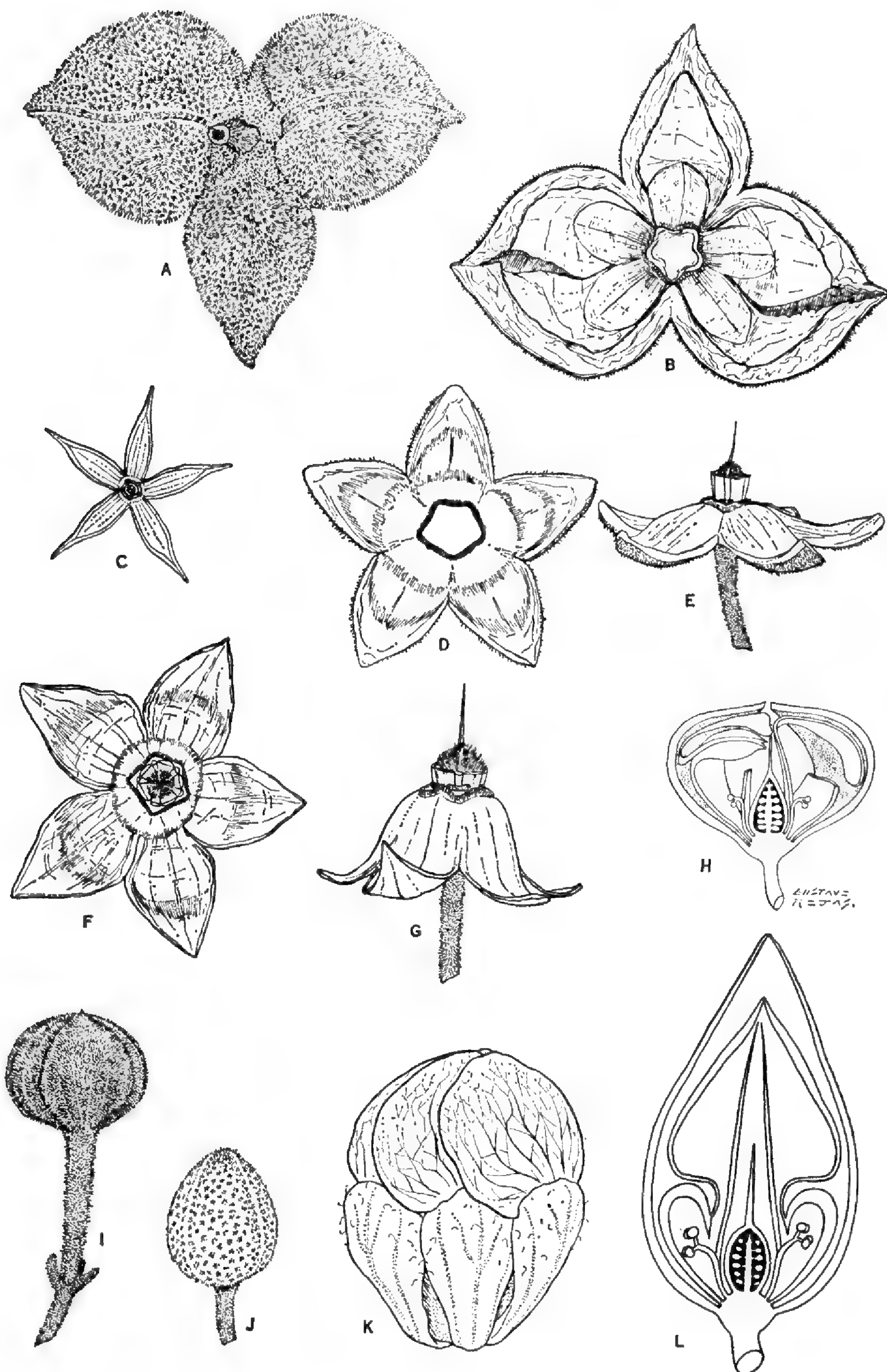


FIGURE 2.—Inflorescence in *Theobroma*: A, caular inflorescence of *T. bernouillii* subsp. *capilliferum* (Cuatr. 16160). B, caular inflorescence in *T. glaucum* (Cope & Hol. 118). C, diagrammatic terminal inflorescence branch in *T. cacao*. D, detail of sympodia. branch of inflorescence in *T. cacao*, diagrammatic, after Stahel. E, inflorescence of *T. cacao*, diagrammatic, after Stahel. F, G, detail of inflorescence in *T. cacao*, diagrammatic, after Stahel. H, inflorescence of *T. bicolor* (Klug 2021). I, diagrammatic inflorescence of *T. bicolor* after Stahel.



[FIGURE 3]

of the cincinnate type. Frequently the branches are very short, forming nodose, articulated sympodia, in which the internodes are hardly noticeable and the bracts appear almost imbricate. Usually the bracts are alternate and the fertile terminal branchlets or peduncles end with 3 bracteoles and one pedicel, the 3 bracteoles corresponding to a theoretical terminal dichasium which develops only the central flower. According to Stahel the peduncles have bilateral, the pedicels radial structure.

The inflorescences may be axillary, in young branchlets, but more often are originated on short, woody branchlets on the trunk and branches; these perennial branchlets form irregular tubercles, sometimes very protuberant, which may form woody branchlets up to several centimeters in length, producing flowering cymes at their ends. The flowers are always pedicellate, the pedicels being relatively long, longer than the reduced branchlets of the cymes.

CALYX (Figs. 3, 4).—The five sepals are valvate and may be almost free and spreading at anthesis or united from one fourth to one half or more of their length; the lower united part is cupular, the free parts are patulous-reflexed at anthesis but finally the whole calyx becomes reflexed, exposing the inner surface. In some instances, the sepals unite 2 by 2 simulating a calyx of 3 lobes, two of them twice as broad as the third. In the section *Andropetalum* the sepals usually are united by three and two and together form a two-lobate cup. The calyx is persistent and its remains may often be seen below premature fruits.

In most cases the sepals are tomentose outside with abundant stellate, ochraceous or ferrugineous hairs, but they may also be puberulous or glabrous, as in species or forms of the sections *Telmatocarpus* and *Theobroma*. In the latter multicellular, glandular, stipitate trichomes are present. The upper or inner surface of sepals is often glabrous or may be more or less pubescent. The inner margin always has a

FIGURE 3.—Calyx and aestivation in *Theobroma*: A, B, calyx of *T. grandiflorum* (Cuatr. 25801) with sepals united by pairs appearing to be trimerous. C, calyx of *T. cacao* (Cuatr. 26004), the sepals spreading, very shortly united at base. D, E, calyx of *T. nemorale* with semispreading and semireflexed sepals, united more than $\frac{1}{4}$. F, G, calyx of *T. chocoense*, with reflexed sepals unequally united in $\frac{1}{3}$ – $\frac{1}{4}$ their length; the basal glandular papillas very conspicuous. H, diagrammatic long. section of bud in *T. cirmolinae* showing the relative position of flower parts in section *Glossopetalum*; at the left side the folded petal (the alternating staminode cut away), at right the staminode (the alternating petal cut away). I, globular bud of *T. chocoense* with valvate aestivation, pedicel, bracteoles and peduncle apparent ($\times 2$). J, ovoid, elongated bud of *T. velutinum* ($\times 2$). K, petals in bud showing the contorted aestivation in *T. velutinum* (Benoist 161), $\times 5$. L, diagrammatic long. section of bud in *T. cacao* showing the relative position of flower parts in sections *Oreanthes*, *Theobroma*, and *Rhytidocarpus*.

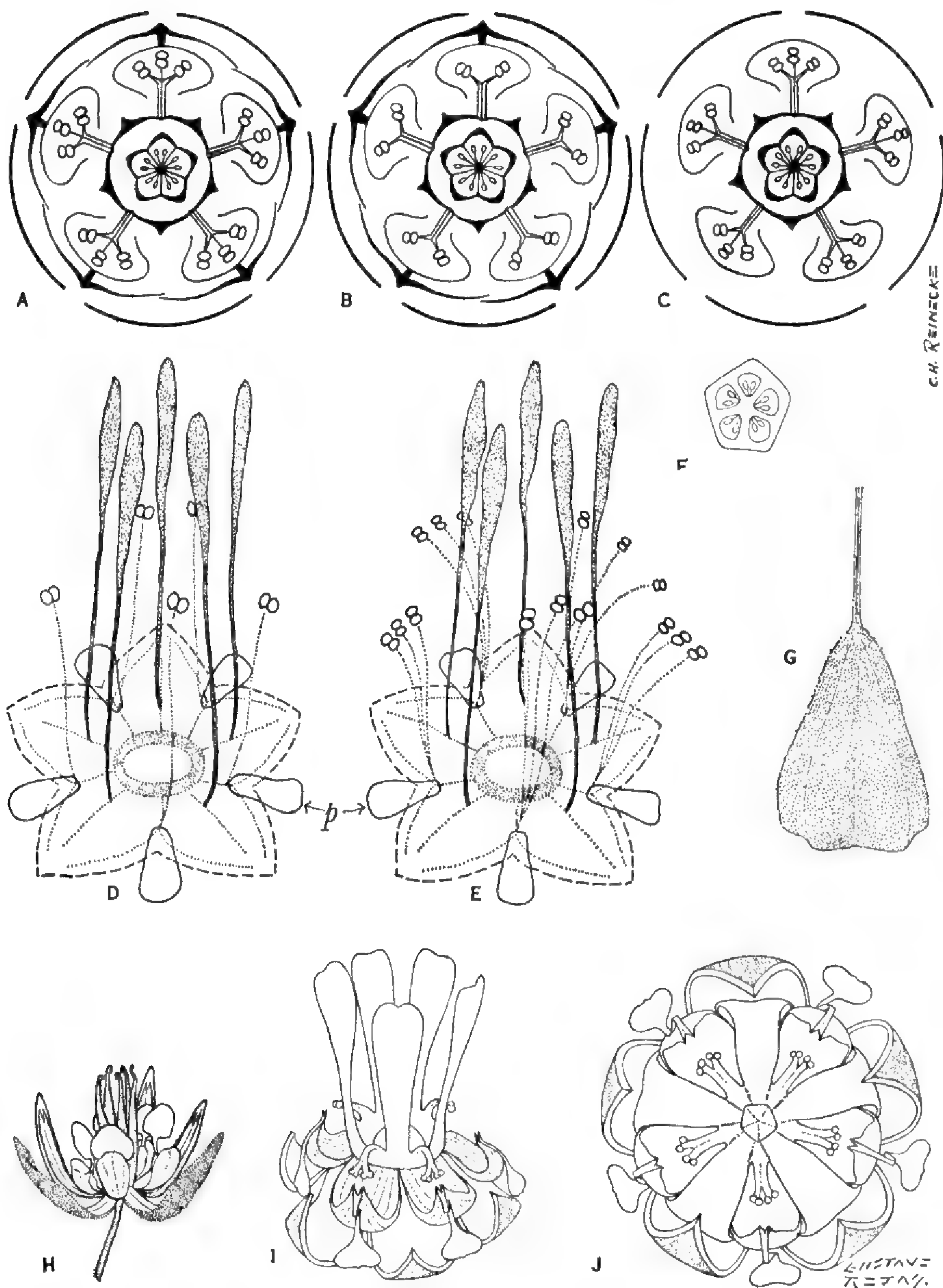


FIGURE 4.—A-C, three types of floral diagrams in *Theobroma*: A, sections *Glossopetalum*, *Andropetalum* and *Oreanthes* (part); B, sections *Theobroma*, *Rhytidocarpus* and *Oreanthes* (part); C, section *Telmatocarpus*. D, basic diagrammatic representation of vascular bundles in the flower of the Byttneriaceae; the marginal vessels (bundles) derive from the vascular branches directed to the petals; the fertile stamens are epipetal, the staminodes episepal; *p*, vascularization of petal in continuous line, after Gazet du Chatelier slightly modified. E, vascular bundles in flower of *Theobroma* (sect. *Glossopetalum*); bundles in stamens branching shortly above the base; adapted from Gazet du Chatelier. F, section of an ovary in *Theobroma* ($\times 20$). G, gynoecium in *T. cirmolinae* ($\times 5$). H, flower in anthesis with spreading sepals in *T. sylvestre* (Ducke 7882), $\times 2$. I, flower in

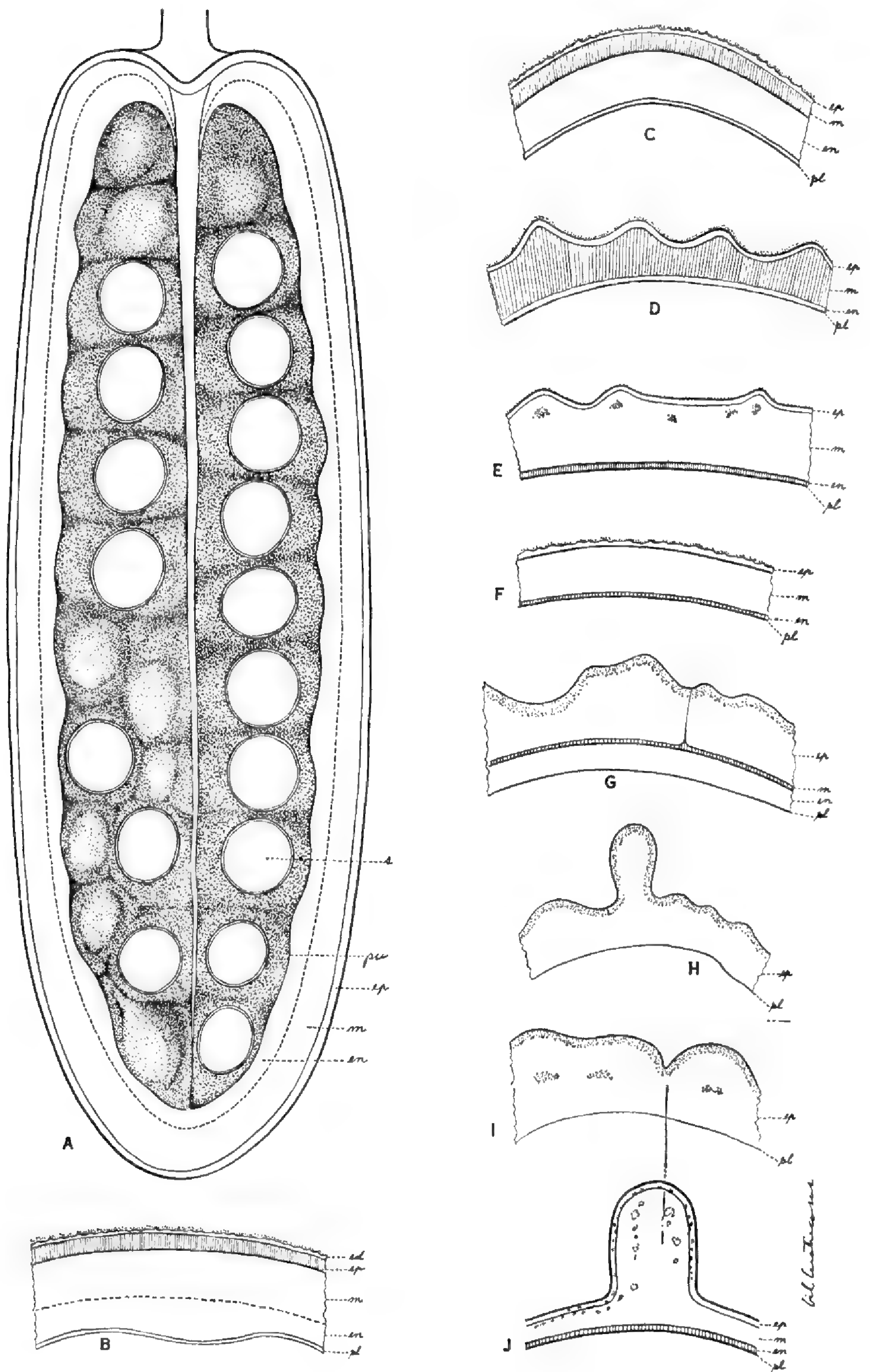
narrow band of extremely minute and dense, whitish, stellate hairs which join the sepals before anthesis. At the base of the sepals, inside, there are commonly glandular, stalked trichomes, which may be very scarce but often are numerous and dense, forming a ring outside the place of petal insertion. These glandular trichomes are lacking in some species or very rare and scattered above on the sepals.

COROLLA (Figs. 3, 4).—The 5 petals are free and uniform; their special feature is that they are strangulated into two very different parts united by a narrow joint. The lower part is cymbiform and erect, rather carnose and rigid, usually 3–7-(or 1)-nerved and has the appearance of a hood rounded at the top; in fact, it represents the claw of the petal, and because of its appearance, it is called the “hood” (*cucullus*). The upper part of the petal (the lamina) is flat, varying in shape from oblong to elliptical or discoid, membranaceous or very thick, yellow, red or purplish. It is almost sessile and directly articulate to the apex of the hood or may be supported by a narrowly laminar pedicel, which is its basal extension; in some species the lamina is lacking or is almost reduced to the pedicellar extension (*T. mammosum*). The petals are dextrorsely contorted in estivation, the laminae being erect when directly articulated to the hood or horizontal and reflexed through the folding of the pedicel. In anthesis the laminae are erect.

ANDROECIUM (Figs. 3, 4).—This is formed by two verticils, which are connate in a tube at the base. The sterile outer whorl has 5 petaloid staminodes, which are subulate, oblong, or obovate, and usually very showy with the same color of the corresponding petal-laminae. They may be erect or reflexed in estivation, and erect, spreading like a star, or reflexed in anthesis; they are thick-membranaceous or carnose and firm, or when subulate or narrowly lanceolate they may have a thick, carnose midrib; they may be glabrous, but more commonly are hairy or covered by minute, muricate trichomes. The inner whorl consists of 5 fertile stamens, with thick filaments which are connate to the tube except for a short (1–3 mm.) free part; the apex is 2- or 3-furcate and each short branch bears an anther. The filaments are spreading and curved and, being opposite the petals, each anther is concealed in the cavity of its corresponding opposite petal-hood. The anthers are 2-celled, and each cell, ellipsoid or almost globose, is unilocular and opens by a longitudinal slit.

The 2- or 3-antheriferous stamens of *Theobroma* have been treated by some botanists as a result of the coalescence of two or three original

anthesis with reflexed sepals, spreading petals and erect staminodes in *T. cirmolinae* (Cuatr. 15336), $\times 2$. 1, flower of *T. cirmolinae* (Cuatr. 15336) initiating anthesis in apical view ($\times 2$).



[FIGURE 5]

stamens. Nevertheless, I consider them to be bifurcate or trifurcate original stamens. The anatomical works of Gazet du Chatelier (1940, p. 278) prove this assertion; at the base of the flower, 5 vascular bundles proceed to the five staminal filaments, these bundles being forked above to serve the two short branches of the filament in *T. cacao*.

GYNOECIUM (Figs. 3, 4).—This is of the coeno-syncarpic type, superior, with carpels opposite to petals. The ovary is 5-celled with axile placentation and many ovules in two rows in each cavity; it is ovoid or ellipsoid, more or less markedly 5-ridged and furrowed, densely stellate-tomentose, or rarely glabrous or covered by stipitate glands.

Stylodes 5, free or more or less adherent to one another, simulating a single style, glabrous, usually about twice as long as the ovary, thin and ending in a punctiform stigmatic apex. The ovules are anatropous with dorsal raphe and two integuments.

FRUIT AND SEED (Figs. 5–7).—The fruit is almost baccate or subdrupaceous and indehiscent, the various types differing in the firmness of the pericarp and in the shape. Almost always there can be distinguished three layers in the pericarp. In the sections *Glossopetalum* and *Andropetalum*, the fruits are externally rigid, hard, the epicarp being woody, about 1 to 2 mm. thick, with an outer tomentose epiderm; the mesocarp is fleshy, differing little in color and firmness from the adjacent endocarp; the inner surface of the latter is a thin but compact membrane; sometimes, the whole endocarp is reduced to this membrane. When the fruit is ripe the carnose inner layers decay or dry, and shrink, but the rigidity of the epicarp maintains absolutely the size and shape of the fruit, keeping the loose seeds inside if they have not been accidentally liberated. In the section *Rhytidocarpus*, the mesocarp is the rigid, woody layer; the epicarp being thinner and carnose, although also with an outer tomentose epiderm; the endocarp is also carnose, and also provided with an inner membrane. In the section *Oreanthes*, typified by *T. speciosum*, the whole pericarp is 5 to 6 mm. thick; the innermost layer, the endocarp, although very thin,

FIGURE 5.—Fruit sections of *Theobroma* species: A, long. section of fruit of *T. simiarum* (Cuatr. 26515A), $\times \frac{1}{2}$. B, transection of pericarp of A, natural size. C, transection of pericarp of *T. grandiflorum*, $\times 1$. D, transection of pericarp of *T. bicolor*, $\times 1$. E, transection of pericarp of *T. gileri*, $\times 2$. F, transection of pericarp of *T. speciosum*, $\times 1$. G, transection of pericarp in *T. cacao* cultivar “cundiamor” (Cuatr. 26492), $\times 1$. H, transection of pericarp in *T. cacao* fma. *pentagonum* (Cuatr. 26540), $\times 1$. I, transection of pericarp in *T. cacao* cultivar “lagarto” (Cuatr. 26004), $\times 1$. J, transection of pericarp in *Herrania cuatrecasana* (Cuatr. 25793), $\times 2$. *ed*, epiderm; *ep*, epicarp; *m*, mesocarp; *en*, endocarp; *pl*, interior pellicule limiting the endocarp inside; *pu*, pulp; *s*, seed.

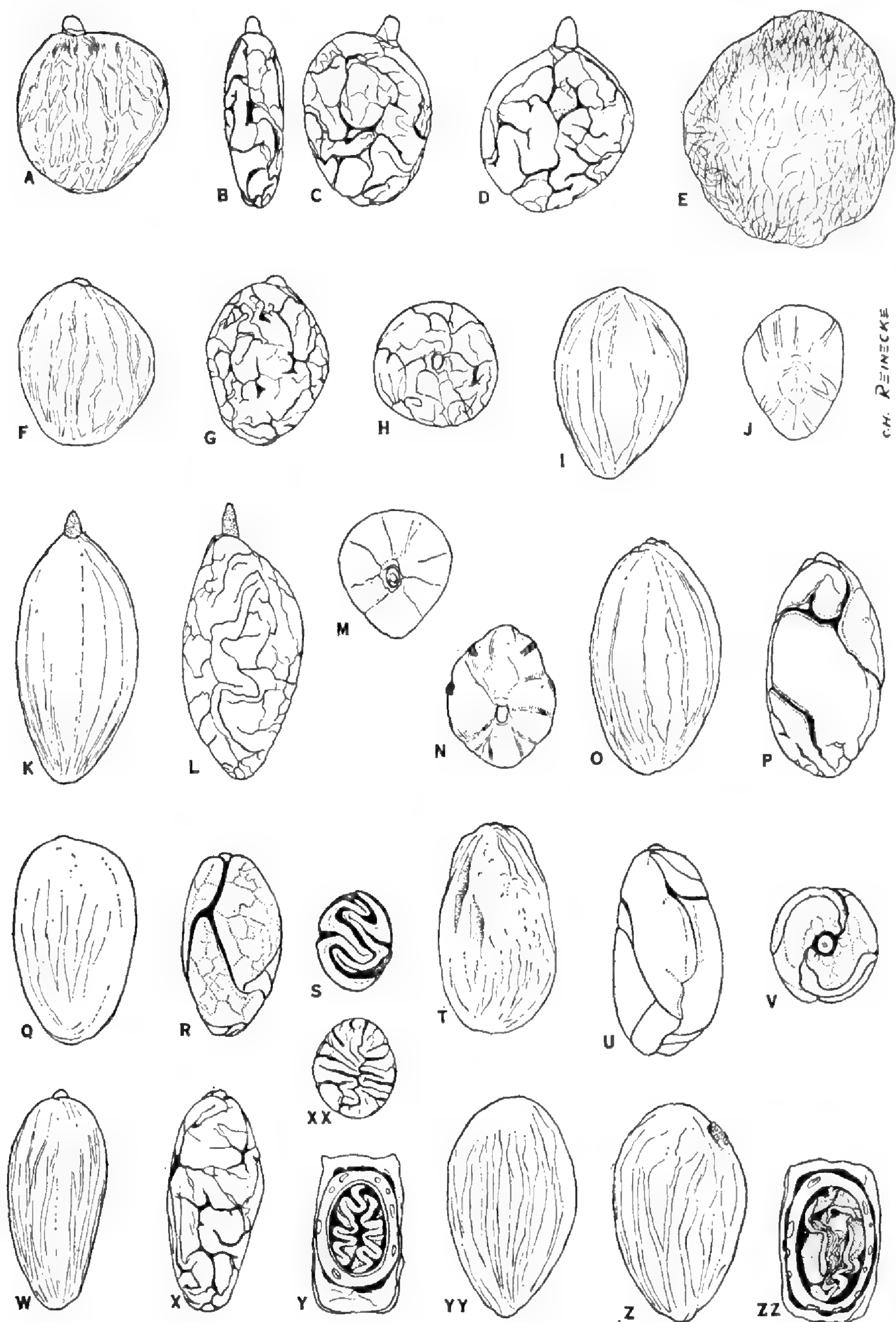


FIGURE 6.—Seeds of *Theobroma*, natural size: A–E, *T. grandiflorum* (Cuatr. 25780T): A, front view of seed stripped from pulp; B, C, D, side and front view of embryo; E, seed surrounded by its pulpy layer. F–H, *T. simiarum* (Cuatr. 26515A): F, seed; G, embryo; H, embryo in apical view. I, J, *T. mammosum* (Cuatr. 25791): seed in lateral and apical

is woody and rigid; the mesocarp is thick and fleshy; the epicarp is also woody but thin and less compact. When the mesocarp dries or decays, the epicarp shrinks slightly, becoming more or less rugose. In the section *Telmatocarpus* the innermost layer, the endocarp, is the most compact and rigid, although thin; the epicarp is coriaceous and thin and the mesocarp is thick and fleshy with strong bundles which build protruding ridges and veins covered by the epicarp. Finally, in section *Theobroma* (Cacao) the fruit is almost baccate because the whole pericarp is carnose; the inner membrane and the outer epiderm may be very firm but the whole pericarp decays easily; it can also dry out, being then coriaceous. Usually the three layers are conspicuous, the epicarp carnose and thick, with glabrous outer epiderm, the vascular mesocarp papyraceous, rigid, thinly woody, and the endocarp carnose, more or less thick, with an inner pellicle; in some forms of cacao the mesocarp may be reduced to a very thin or discontinuous layer or to isolated vascular bundles (fig. 5r); rarely the endocarp is reduced to the inner pellicle (fig. 5h, forma *pentagonum*). Usually, the dorsal vascular bundles of each carpel develop into transverse membranes within the fleshy epicarp connecting with the mesocarpial layer. Gummy sacs are always present in several parts of the pericarp.

The young fruit, as well as the ovary, has five cavities with the incipient seeds arranged in one or two rows in each cavity. At maturity the cell walls vanish and the seeds with their thick outer pulpy layer fill the single cavity, arranged usually in five rows.

The shape and size of the fruit are variable and they are, combined, specific characters except for cultivated cacaos. The fruits range between 6 and 35 cm. long by 5 to 12 cm. broad and may contain, when ripe, from 16 to 60 seeds. They may be ellipsoid, globose, ovoid, oblong, or fusiform, with rounded or attenuate ends, with completely smooth surface like a potato or marked more or less with 5 or 10 ridges, or they may be echinate or verrucose. In all cases they are indehiscent and the liberation of seeds follows the decay of the shell, which in many cases, as in those with hard, woody pericarp, may take so long that the seeds have died. The common natural way of propagation of the seeds is accidental, usually by

view. k-m, *T. angustifolium* (Cuatr. 25790): k, seed stripped from pulpy layer; l, embryo; m, embryo in apical view. n-p, *T. gileri* (Cuatr. 26167): n, seed in apical view; o, same laterally; p, embryo. q-s, *T. speciosum*: q, seed; r, embryo; s, embryo in transection, showing the folding of cotyledons. t-v, *T. bernouillii* subsp. *capilliferum* (Cuatr. 17034): t, seed; u, embryo; v, embryo in apical view. w-xx, *T. cacao* fma. *pentagonum* (Cuatr. 26004): w, seed; x, embryo; xx, transection of embryo. y, yy, *T. cacao* fma. *pentagonum* (Cuatr. 26540): y, transection of seed with episperm and pulp; yy, seed. z, zz, *T. cacao* cultivar "cundiamor" (Cuatr. 26492): z, seed; zz, transection of seed with episperm and pulp.

animals (mostly monkeys, but also squirrels, rats, and other animals) which break the pericarp in order to suck the pulp surrounding the seeds, which may be expelled later in other places, thus disseminating the seeds (fig. 5).

The fruits, which are commonly called pods in English, *mazorcas* in Spanish and *cabosses* in French, may stay on the tree or fall down after maturation; in the latter case, they may fall with the peduncle (e.g., *T. bicolor*) or without it (as in *T. grandiflorum*). Precise observations in many species are wanted.

The seeds are ellipsoid, ovoid or amygdaloid, more or less irregularly compressed, complanate, or terete, and range from 15 to 40 mm. long and 10 to 22 mm. broad; the integuments or skin form two strata with an additional outer, thick, gelatinous-pulpy layer surrounding them. The testa is generally thick and subcoriaceous, with an external epiderm covered by a thick cuticle, a thick layer of polyhedral and mucilaginous cells, and an inner layer of sclerosed cells. The inner tegument is a thin membrane of several layers of thin-walled, complanate cells. Inside, the large embryo is composed of two large, thick, strongly folded and corrugate cotyledons and a straight, rather thick, terete radicle, the plumule being scarcely developed. The endosperm at maturity has the shape of a very fine pellicle, containing scattered cells with calcium oxalate, covering the embryo outside and between its foldings. The cotyledons possess an epiderm, often with scattered, stipitate glandular trichomes and a main cellular tissue rich in starch, fat, aleurone, tannoid and alkaloidal substances, among these the important theobromine compounds. In most species the cotyledons are white, but in a few they are violet, reddish, purplish, being stained by tannins (figs. 5, 6). Germination may be either epigeous or hypogeous according to the species (fig. 7).

The pulp surrounding and united to the seeds is white, yellowish, or yellow, and often sweet and aromatic and palatable, but it may be also scentless and tasteless to men; it is, however, always appreciated by animals, which hunt the pods, extract the seeds to suck the pulp, thus disseminating them.

In appropriate conditions the pulp suffers a fermentation process which separates it from the seed; during that fermentation, very well known in the case of *T. cacao*, chemical changes take place inside the embryo developing a special aroma. In the industry of cacao torrefaction completes the desired effects of fermentation.

Premature fruits keep their viability for some time provided they are protected against loss of humidity and stored under suitable temperatures (20–25° C.); when ripe, the seeds become immediately ready for germination; they may germinate inside the pods. The

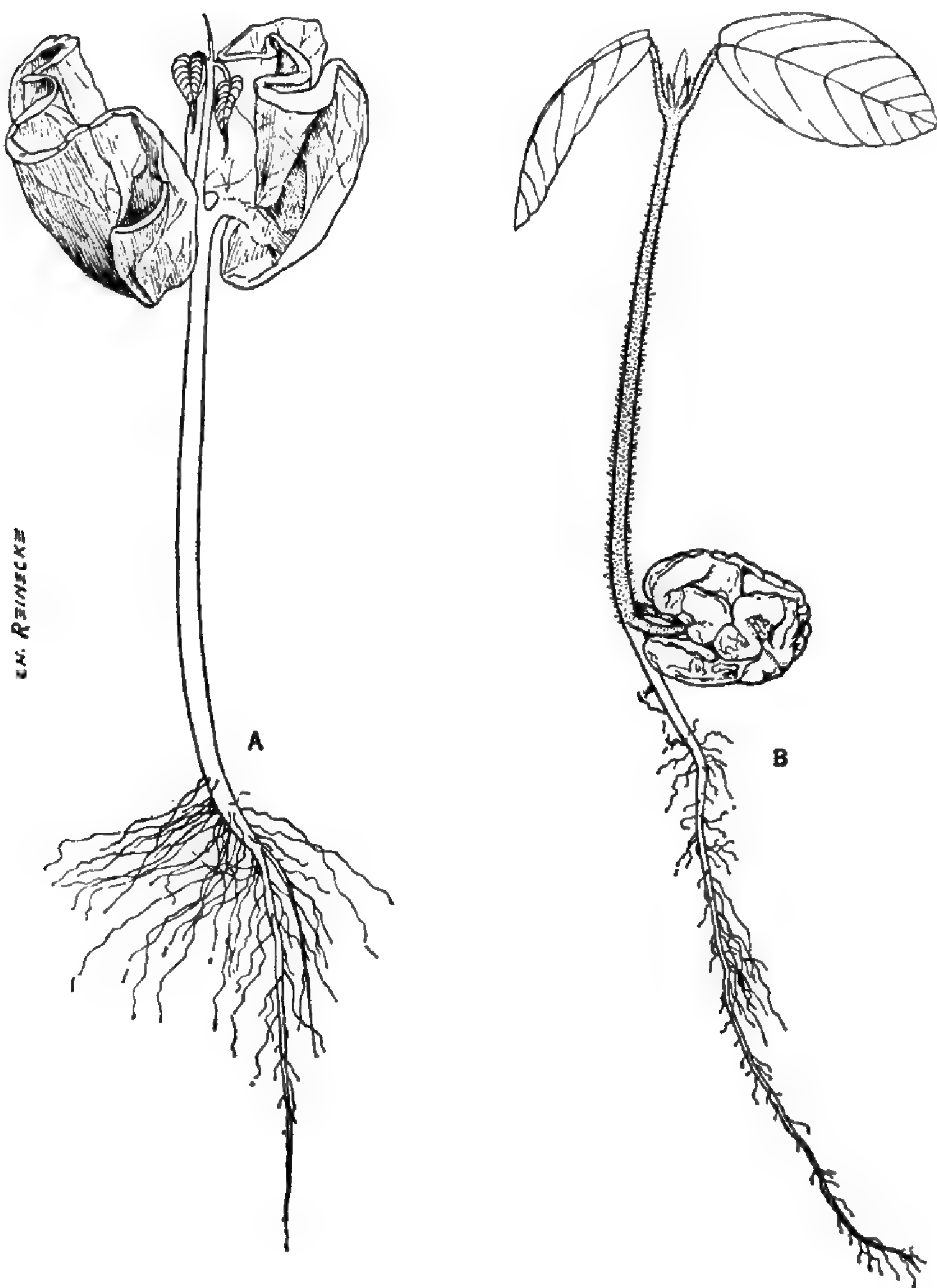


FIGURE 7.—A, Epigeal germination in *Theobroma bernouillii* subsp. *capilliferum* (Cuatr. 17350A). B, Hypogeal germination in *T. grandiflorum* (Cuatr., Cope & Bart. 25780A).

germinating power of *Theobroma* seeds lasts only for a short time, a few weeks; observations on *T. cacao* have shown a maximum extension time of viability to about three months, when carefully preserved in their pods or under special protection. They are extremely sensitive to the degree of humidity, which has to be kept high, and to low temperatures. Recent experiments in Turrialba showed that cacao seeds could not resist low temperatures for even a short time; seeds exposed for 16 minutes at 8° C. lowered the germinating capacity to 6%, and 4 minutes exposure at 2° C. inhibited germination almost completely (Hunter, 1959; Hunter & Boroughs, 1961). This may be the explanation why cacao seeds lose their germinating power

when transported by airplanes at high altitude (Hunter, personal communication).

Ecology

Theobroma is a tropical American genus restricted to the lower tree-story of the evergreen rain forests. The species demand a high degree of mean annual temperature with narrow oscillations, a constant high humidity, and protection (shade) against direct radiation and evaporation. Several species are often found at the edges of rivers or marshes in more or less temporarily flooded areas; others always grow on elevated, drained places. They like relatively rich and neutral soils. These conditions are found only in the warm, wet, forested, equatorial regions between latitudes 18° North and 15° South, with temperatures of 20° to 30° C., with a minimum of 16° and maximum of 40°. A few species grow at higher altitudes up to 1250 meters, being able to withstand minimum temperatures of 14° and even 12° C. Where *Theobroma* is at home, the rainfall is from 2000 mm. to 8000 mm. annually or even higher, and is more or less evenly distributed throughout the year. *Theobroma* does not resist even short dry seasons without the protection of dense shade and local humidity. In cultivation *T. cacao* can endure less humid climates, and more open lighter spots especially when irrigated, and somewhat lower temperatures than the normal optimum. So the area of cultivated cacaos may extend far above 20° North and below 20° South of the Equator. Not only the *Theobroma* trees but also the seeds are highly specialized to the humid equatorial ecological conditions. It is known that the seeds keep for a very short time their capacity for germination, which often takes place inside of the pod; only under high humidity and optimum temperatures can they maintain their viability (see above).

Geographic Distribution

The genus *Theobroma* is a typical neotropical genus, distributed throughout the rain forests of the western hemisphere between latitudes 18° North and 15° South. Some species have a broad range of distribution, like *T. subincanum*, which is spread throughout the Amazon-Orinoco basins, being one of the most ancient of the genus. The elevation of the Andes in the early Tertiary separated populations of *Theobroma* previously widespread before, favoring speciation through isolation. Vicarian species separated by this way are *T. subincanum* (east of the Andes) and *T. hylaeum* (west); *T. microcarpum* (east) and *T. gileri* (west). The complexity of the mountains of the northern part of Colombia through Central America was also an isolating factor which favored speciation in that part of the hemisphere where regional or local endemics are present. Maps 1 and 2 are self-explanatory.

Pollination

Although transportation of pollen by the wind has had some acceptance, it seems that only pollination by insects has been proved. Works by Harland, Stahel, Posnette, Saunders, Cope, Uzel, Jones, and Pound, have demonstrated that several kinds of flying and crawling insects are involved in pollen transportation, among them thrips, ants, midges, and aphids. Experiments by Cope proved that *Frankliniella parvula* Hood and *Wasmannia auropunctata* Rog. were mostly responsible for pollen transportation in Trinidad. Saunders found in Costa Rica that *Forcipomyia* midges performed pollination in cacao. The aphid *Toxoptera aurantii* Fouse is also recorded as a pollinating agent.

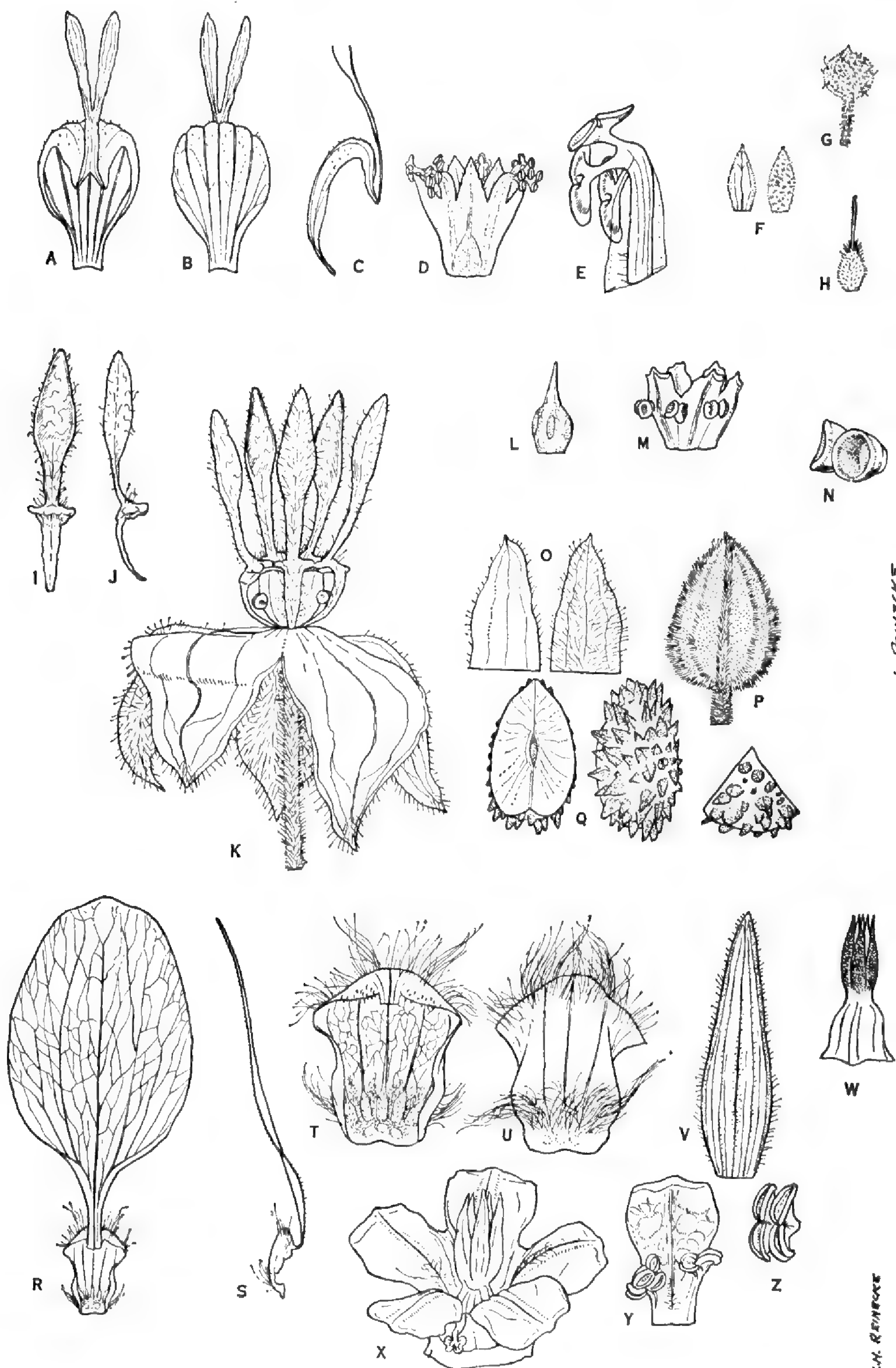
Relationships

The basic features of *Theobroma* are: Flowers bisexual, pentamerous; sepals valvate; petals strangulated, contorted in bud with cymbiform, cucullate lower half; 5 stamens opposite to petals and 5 evident, alternating staminodes united in a short basal tube; stamens shortly 2-3-branched; anthers 2-celled; ovary superior, 5-celled; ovules many, anatropous with 2 integuments; fruit subdrupaceous or subbaccate; seeds with pulpy envelope; cotyledons folded, corrugate; evergreen trees with dimorphic branching and dimorphic, entire, alternate leaves. This diagnosis places the genus in the family Sterculiaceae (fig. 8).

Theobroma exhibits a unique set of characters which makes it a very "natural" genus. However, some of the outstanding features of its floral structure are also shared by other genera, the most conspicuous being the cucullate or concave lower part of the petals which define the tribe Byttnerieae DC., and determine the close relationships between its members: *Byttneria*, *Ayenia*, *Rulingia*, *Commersonia*, *Theobroma*, *Guazuma*, *Herrania*, *Abroma*, *Glossostemon*, *Scaphopetalum*, and *Leptonychia*. In most of these cases the similarity with *Theobroma* in the flower structure (petals, androecium-tube, staminodia, and position of anthers) is so obvious that it was noticed since early times. The first historical association of *Theobroma* to another genus was by Linnaeus who joined it with *Guazuma* under Polyadelphia Pentandria. Lamarck (1785) was the first to make a family associating *Theobroma* with *Abroma*, *Guazuma*, *Ayenia*, *Byttneria*, and *Kleinhovia*. Jussieu (1789), associated *Theobroma* with *Abroma*, *Guazuma*, *Byttneria*, *Dombeya*, *Assonia*, *Pentapetes*, and *Melhania* in sectio V [bis] of ordo XIV. Kunth (1823) was the first to establish critically the main groups of the Sterculiaceae, one of them the Byttneriaceae verae including *Theobroma*, *Guazuma*, *Abroma*, *Glosso-*

stemon, *Byttneria*, *Ayenia*, and *Commersonia*. This grouping was basically followed by DC. (1824), Endlicher (1840), although he separated the Sterculiaceae from Byttneriaceae, Baillon (1873) in his series Byttneriées, Bentham & Hooker (1862), who enlarged the family to 7 tribes, and Schumann (1890) who enlarged it to 8 tribes. The latter botanist, who made an outstanding contribution to the comparative morphology and taxonomy of the whole family, did not alter the concept of the Byttnerieae DC. as presented by Bentham and Hooker. Recent workers, like Gazet du Chatelier (1940), who made broad comparative anatomical and morphological studies in the Sterculiaceae, found good reasons to keep Schumann's basic taxonomic approach.

Bentham and Hooker divided the tribe artificially in two groups which were named by Schumann Theobrominae and Byttnerinae, with respectively 2-3-antheriferous and 1-antheriferous stamens. On the other hand, the four genera of Byttnerinae differ from *Theobroma* also because *Byttneria* has spirally convolute cotyledons, short, dentiform staminodes and linear, rather thick, petal-laminae; *Ayenia* has very long, linear petal-claws, trilocular anthers, and spirally convolute cotyledons; the Old World *Commersonia* and *Rulingia* have a pitcher-shaped petal base and flat cotyledons. From the other Theobrominae genera, *Theobroma* is distinguished by the special structure of the petals, staminodia, and vegetative system; the Persian genus *Glossostemon* is a shrub with hairy, dentate leaves, ovate-oblong petals, concave at base, and with many short stamens connate to the basal part of the staminodes; the Old World *Leptonychia* differs by its short, squamiform petals, fertile stamens with filaments much longer than the staminodes, and flat cotyledons; the west African shrub *Scaphopetalum* has exappendiculate petal hoods, a campanulate androecium with shortly triangular staminodes and sessile 3-grouped anthers; the tropical American *Guazuma* differs, besides in the fruit, by the long, bifid petal appendages, the spirally convolute cotyledons, and the vegetative structure, the leaves being serrate; *Abroma*, an oriental genus spread from eastern India through the Pacific islands to Australia, is similar to *Theobroma* in the floral arrangement but usually has more developed petal laminae, shorter petaloid staminodes, subsessile anther groups, flat cotyledons, a different vegetative habit, and usually cordate, more or less lobate, hairy leaves. Moreover, all genera mentioned of the Byttnerinae differ from *Theobroma* by their capsular, generally dehiscent fruit. Only *Theobroma* and *Herrania* in the tribe have an indehiscent baccate or subdrupaceous fruit. For this reason, Schumann united them, calling the latter section *Herrania*, an arrangement adopted by other botanists, such as Pittier and Ducke. Nevertheless, Bernoulli, the monographer who



[FIGURE 8]

C. M. REINHOLD

C. M. REINHOLD

went deeply into the genus, and Chevalier in his revision consider *Herrania* and *Theobroma* different genera. R. E. Schultes followed the same line in monographing, after long experience, the genus *Herrania* with 17 species. They are undoubtedly two well-defined, independent genera.

Herrania, *Abroma*, *Guazuma*, and *Byttneria* surely are the genera closest to *Theobroma*. Chromosome number and palynology help to determine relationships. The chromosome number is identical for *Theobroma* and *Herrania*, $2n = 20$ but it is $2n = 16$ for *Guazuma* and $2n = 14$ in *Byttneria* (Cristóbal); data for *Abroma* not available. The pollen grains are suboblate in *Theobroma*, prolate in *Herrania*, prolate-spherical in *Guazuma*, and oblate in *Abroma*.

Because of the similarity of the fruits and the confusion which had prevailed in the past between *Theobroma* and *Herrania*, their differences are summarized here as follows:

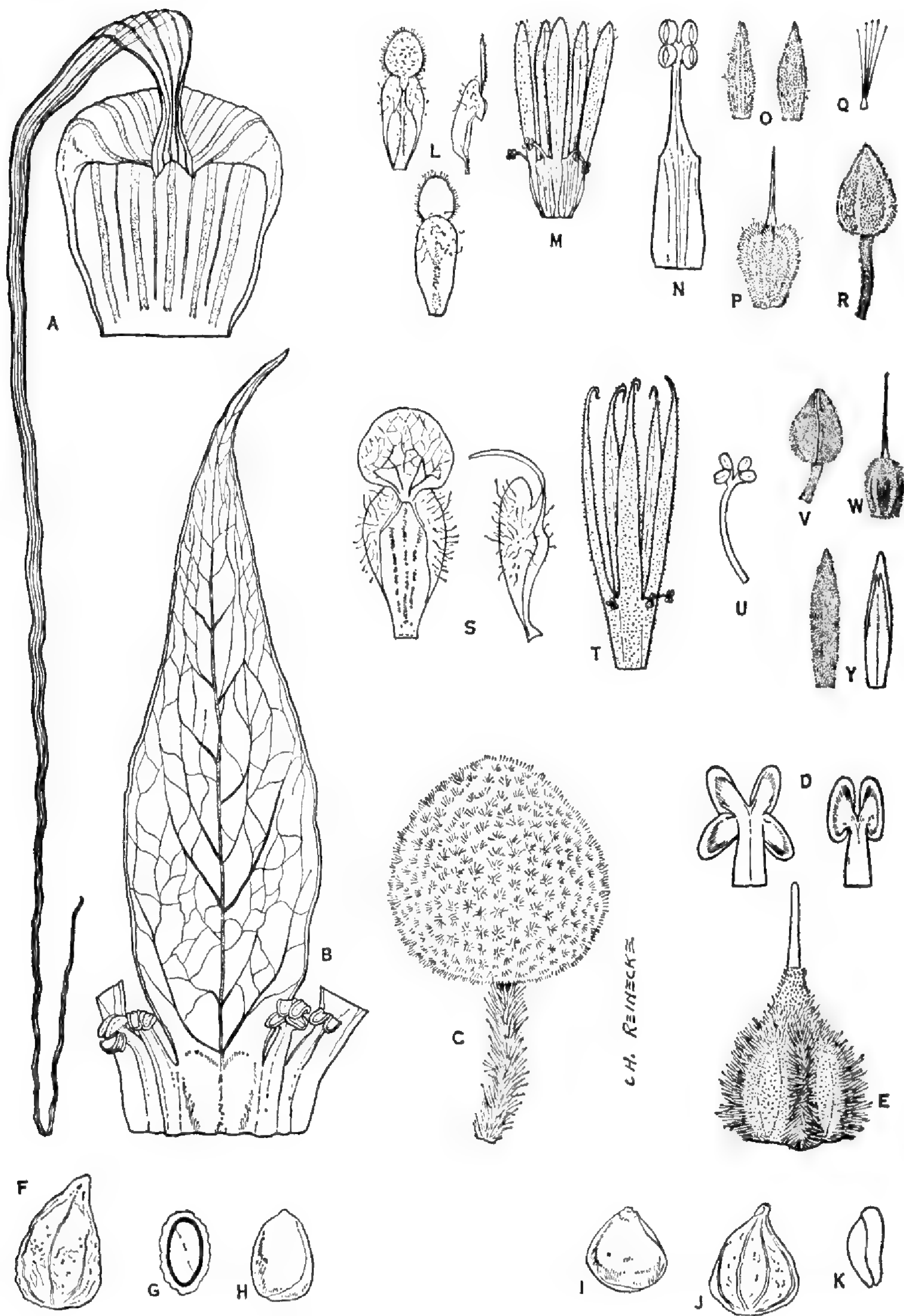
Theobroma. Stem sympodial, with 3-5-verticillate branching; branches dimorphic; branching copious; leaves dimorphic; leaf-blades simple, entire; petal lamina more or less rounded to lanceolate, not more than twice as long as the hood, erect or inflexed and contorted in aestivation; pollen grains suboblate; cotyledons strongly folded and corrugate; fruit usually smooth or rugose, angular, seldom strongly costate; staminal filament symmetrically and shortly 2- or 3-furcate at apex.

Herrania. Stem monopodial, unbranched, with apical growth; leaves uniform, 5-9 digitate, long-petiolate, in a terminal, lax cluster; petal lamina many times longer than the hood, linear, pendulous in anthesis, involute in aestivation; pollen grains prolate; cotyledons thick, flat or very slightly folded; fruit usually strongly costate; staminal filament usually asymmetrically parted in two branches, one 1-antheriferous, the other 2-antheriferous (fig. 9).

Evolution

The question of how the genus *Theobroma* may have originated is a speculative matter on which botanists like Schumann (1886)

FIGURE 8.—Genera related to *Theobroma*: A-H, *Guazuma*: A, articulated and hooded petal with bifid appendix, from inside; B, same from outside; C, same in lateral view, $\times 5$; D, androecium, $\times 5$; E, fertile stamen, $\times 20$; F, sepals, $\times 2$; G, bud; H, gynoecium, $\times 5$ (*G. tomentosa*, Cuatr. 22942). I, J, *Byttneria*: I, articulated petal from inside, $\times 10$; J, same laterally. K, flower, $\times 10$. L, gynoecium, $\times 10$. M, androecium, $\times 10$. N, detail of the anther, $\times 20$. O, sepals, from inside and outside, $\times 5$. P, bud, $\times 5$. Q, carpel of fruit from inside, outside and apical view, $\times 2$ (*B. arguta*, Cuatr. 8226). R-Z, *Abroma*: R, articulated, hooded petal, $\times 2$; S, same in lateral view; T, hood from inside and U, from outside, $\times 5$; V, sepal, $\times 2$; W, pistil, $\times 5$; X, androecium surrounding the gynoecium, $\times 5$; Y, base of staminode with laterally attached stamens, $\times 5$; Z, biantheriferous stamen, $\times 10$ (*Abroma augusta*, Sulit 18880).



[FIGURE 9]

did not want to take a stand. Edlin (1935) who developed a theory on the evolution of the Malvales, considers the family Sterculiaceae limited to the tribe Sterculieae, all other groups forming the family Byttneriaceae; he considers the stamens the result of union. Gazet du Chatelier (1940), after a detailed examination of the Sterculiaceae, came to the conclusion that there was an original unknown type from which were derived two diverging groups (subfamilies or families), the "Eriolaenées" and the "Buettneriées," but he did not go much further in his speculative evolution; the stamens of *Theobroma* are considered as branched by him.

All the genera of the Byttnerieae are similar and probably originated at the same time evolving from an original unknown type; they diversified their flowers and the leaves, probably through mutations aided by geographical and ecological barriers. The parts have evolved independently, e.g., *Rulingia* has undivided fertile stamens, a more ancient character, but pitcherlike petals, a more evolved one. Conversely, *Leptonychia* has simple, more primitive petals but exhibits branched stamens, a more advanced character. *Byttneria* and *Guazuma* have elaborate, advanced petals but less developed staminodes; *Commersonia*, as well as *Abroma* and *Theobroma*, have more advanced petals and staminodes than the other genera. *Scaphopetalum* is an example of a more advanced type due to the loss of the petal lamina and reduction of the staminodes. Even if we can attribute primitiveness or the contrary to some characters, it is not possible to draw a lineal series of genera according to antiquity. Nevertheless, I would venture to say that *Theobroma* and *Herrania* belong to the most modern in the Byttnerieae because of the structure of the fruit, with thick and partly or totally carnose pericarp and delicate, short-lived seeds. These may be characters acquired in the process of evolution and kept by their adaptation to the extremely hot and humid ecological conditions of the tropical American forests. It also seems to me that *Herrania* is a more evolved genus in regard to the flower, but not in the simplicity of the monopodial, juvenile-

FIGURE 9.—A-H, *Herrania pulcherrima* v. *pacifica* (Patiño 23): A, articulated and hooded petal, $\times 5$; B, segment of androecium with a staminode and the adjacent stamens, $\times 5$; C, bud, $\times 5$; D, stamens, $\times 10$; E, gynoecium, $\times 5$; F, seed, $\times 1$; G, transection of seed, $\times 1$; H, embryo, $\times 1$. I-K, *H. cuatrecasana*: I, embryo; J, seed; K, transection of embryo, $\times 1$. L-R, *Theobroma bicolor* (Garcia B. 11178): L, petal from inside, outside and laterally, $\times 5$; M, androecium, $\times 5$; N, fertile stamen and part of staminal tube, $\times 10$; O, sepal from inside and outside, $\times 2$; P, gynoecium, $\times 5$; Q, styles, $\times 5$; R, bud and pedicel, $\times 2$. S-Y, *T. sylvestre* (Ducke 7882): S, petal from inside and laterally, $\times 5$; T, androecium, $\times 5$; U, stamen, $\times 10$; V, bud, $\times 2$; W, gynoecium, $\times 5$; Y, sepal from outside and inside, $\times 2$.

like, unbranched stems, in the digitate, loosely clustered leaves, and inseparable, hypogeous cotyledons, due probably to the stringent ecological conditions of the shadowy underlayer of the humid tropical forest. Aside from *Herrania*, the sections of *Theobroma* (*Glossopetalum*) with pseudoterminal growth, may be more primitive than the ones (*Oreanthes*, *Rhytidocarpus*, *Theobroma*) which have lost the axillary buds of the jorquette branches, necessitating lateral shoots to continue growing. The section *Theobroma* may be more evolved than the others on account of the 5-branching system and carnose fruits. The section *Telmatocarpus* may be more advanced in another direction because of the reduction or absence of the petal lamina and the discontinuity of the vascular, woody system in the pericarp, which is only partially woody and more vulnerable. The parallelism in evolution of the sections *Theobroma* and *Telmatocarpus* is seen in the glabrous or almost glabrous leaves, more suited to rain-forest ecology. The section *Rhytidocarpus* may be an ancient type with less showy petals and staminodes, axillary flowers, and a thick-woody pericarp.

No fossils belonging to *Theobroma* have been recorded.

The geographic distribution does not give any solution to these questions of evolution because almost all sections are represented at both sides of the Andes. It seems that the richest region in species is around Panama and Colombia, where species with a very restricted area are found, especially if we consider this region extended to Costa Rica. I feel that *Theobroma* is a genus with a marvelous set of characters controlled perhaps by independent genes, which seemingly can combine independently resulting in many different sets of combinations.

Economic Uses

The seeds of *Theobroma* are rich in starch (15%), protein (15%), and oil (50%), for which reason they are considered a substantial food. Moreover, they have a volatile oil (cacao-essence) which gives an aromatic flavor and 1.5 to 3% of theobromine, an alkaloid known for its stimulant properties. Caffeine is also present in *Theobroma* seeds. Both alkaloids have been found in the seeds and leaves of *T. bicolor*, *cacao*, *grandiflorum*, *microcarpum*, *obovatum*, *speciosum*, *sylvestre*, and *subincanum* (Willaman and Schubert, 1961). The cacao seeds contain also a red pigment, tanine, and small quantities of malic and tartaric acids, asparagine, and coline.

It is not necessary to emphasize the economic importance of the industry in cocoa and chocolate. Most of the wild species of cacao are often used by the natives, who suck the pulp or prepare refreshing drinks with the pulp. The seeds of most species may serve for the preparation of chocolate, but actually only one species has become

commercially important in this respect, *T. cacao*, which is the only one widely cultivated. An important secondary product from cocoa seeds is the cocoa butter extracted by pressure during the process of making chocolate. Cocoa butter is important in cosmetics and pharmaceutical industries. Cacao extracts and theobromine are important in medicine because of their cardiotonic and diuretic properties.

The wood of several *Theobroma* species is important in local construction and because of its toughness and strength is very much used in the manufacture of tools and parts of instruments and machines.

Anatomy of the Wood

CONTRIBUTED BY WILLIAM L. STERN¹

This study of the wood of *Theobroma* is based largely on microscope slides borrowed from the S. J. Record Memorial Collection of woods at Yale University and from the wood collection of the Imperial Forestry Institute at the University of Oxford in England.² It is regrettable that among these slides, only 9 species were present (table 1). However, the description of the wood probably represents a fairly good outline of at least the qualitative aspects of the microscopic structure, and is sufficiently complete to enable comparisons between *Theobroma* and other genera to be made.

It is evident from this brief study that noticeable variation occurs in the wood anatomy of different specimens of the same species. In this regard it is interesting to note that Record and Hess (1943, p. 517) were impressed with the structural variation in rays in different parts of the same specimen in their study of the woods of Sterculiaceae. As a whole, however, the wood of *Theobroma* species does not present any characters of significant anatomical import which would enable us to separate them on anatomical grounds. Chattaway (1937) also found this to be true of the genera she studied in her investigation of the Sterculiaceae (sensu Edlin 1935).

¹ REFERENCES:

- Bailey, I. W. The problem of differentiating tracheids, fiber-tracheids, and libriform wood fibers. *Trop. Woods* 54:18-23. 1936.
- Bentham, G., & Hooker, J. D. Sterculiaceae, in *Genera plantarum*. 1:214-228. London, 1862.
- Chattaway, M. Margaret. The wood of the Sterculiaceae. I. Specialisation of the vertical wood parenchyma within the sub-family Sterculieae. *New Phytol.* 31:119-132. 1932.
- . Ray development in the Sterculiaceae. *Forestry* 7:93-108. 1933.
- . The wood anatomy of the family Sterculiaceae. *Phil. Trans. Royal Soc. London, Ser. B-Biol. Sci.* 228:313-366. 1937.
- Edlin, H. L. A critical revision of certain taxonomic groups of Malvales. *New Phytol.* 34: 1-20. 1935.
- Metcalfe, O. R., & Chalk, L. *Anatomy of the dicotyledons*. 1:251. Oxford, 1950.
- Record, S. J., & Hess, R. W. *Timbers of the New World*. p. 517. New Haven, 1943.

² I would like to thank Dr. Graeme Berlyn of Yale and Dr. L. Chalk of Oxford for their kindness in making slides available for study.

The imperforate tracheary elements are all fiber-tracheids; that is, the bordered pits are smaller in diameter than those found in the walls of vessel elements in the same species. Bordered pits usually show extended inner apertures; these may be crossed or not. The wall thickness varies from thick to thin, sometimes even within the same species (cf. specimens of *T. bicolor*).

Pores are distributed mainly in the solitary configuration on the transverse section (34–86 percent; average 62 percent); radial multiples are next in abundance (8–47 percent; average 33 percent) and pore clusters are least abundant (0–10 percent; average 4.5 percent). In different specimens of the same species, dissimilarities may occur; for example, in *T. obovatum* (Williams 161), solitary pores account for 86 percent of the pores per field, whereas in *T. obovatum* (Williams 230), they account for only 57 percent of the pores per field. Perforation plates are entirely simple. Vessel element end walls form angles from 45° to 80° with the vertical. Intervascular pitting is alternate. The

TABLE 1.—*Specimens examined in anatomical analyses*

Species of <i>Theobroma</i>	Collector and No.	Origin	Herb. voucher	USw No.*	Yw No.	FHow No.
<i>angustifolium</i> DC.	Cooper & Slater 242	Panama	Y	30	10595	3502
<i>bernouillii</i> Pitt.	Pittier 4105	Panama	US			
<i>bicolor</i> H. & B.	For. Dept. Br. Hond. H. 2192/29(?)	British Honduras	F			5632
<i>bicolor</i> H. & B.	"Ford-Brazil 397" (?)	Brazil	F		22075	6998
<i>bicolor</i> H. & B.	Ll. Williams 2149	Peru	F		17804	7008
<i>bicolor</i> H. & B.	Ll. Williams 3346	Peru	F		18176	7007
<i>cacao</i> L.	"L. 3225 (via Hamburg)"	South America				5703
<i>cacao</i> L.	Vigne 2433	Ghana	Kumasi; K(?)			6898
<i>grandiflorum</i> (Willd.) Schum.	Ll. Williams 2401	Peru	F		17893	7001
<i>microcarpum</i> Mart.	Krukoff 6203	Brazil	US		36510	
<i>obovatum</i> Klotzsch ex Bernoulli	Ll. Williams 161	Peru	F		71232	7010
<i>obovatum</i> Klotzsch ex Bernoulli	Ll. Williams 230	Peru	F		17263	7011
<i>sylvestre</i> Mart.	Ducke 103	Brazil	Y		21362	7009
<i>subincanum</i> Mart.	Ll. Williams	Peru	F		17578	7000
<i>subincanum</i> Mart.	Ll. Williams	Peru	F		18144	6999

* Abbreviations from W. L. Stern & K. L. Chambers. The citation of wood specimens and herbarium vouchers in anatomical research. *Taxon*, 9: 7–13, 1960.

bordered pits are frequently crowded and their outlines markedly angular. Other times the pits are rounded to elliptical. Vessel-axial parenchyma pitting and vessel-ray parenchyma pitting generally follow the pattern of the intervacular pitting. Occasionally pits may be elongated or slightly irregular. No deposits or tyloses appeared in any vessels.

Both uniseriate and multiseriate vascular rays occur in each of the specimens examined. Multiseriate rays may be up to 20 cells wide (in *T. sylvestre*), but a width of 10 to 15 cells is more common. Uniseriate rays are much lower in height than multiseriate rays; the latter range from 30 to 230 cells high. There is often evidence of dissociation of these broad, high rays into lower, narrower rays by the "intrusive action" of fiber-tracheids while the cells are still in a plastic stage. Many of the multiseriate rays are characterized by the presence of sheath cells, e.g., in *T. obovatum* (Williams 161); however, they never form complete sheaths about the rays and are rare in some specimens. Multiseriate rays are heterocellular, with the multiseriate portion comprising procumbent cells, and uniseriate, alate extensions of 1 to several (15+) upright or square cells; uniseriate rays are usually homocellular composed of square or upright cells and sometimes occasional procumbent elements. The ray cells are commonly characterized by deposits of reddish or yellowish, non-staining materials.

Axial parenchyma occurs in two dispositions: apotracheal, as diffuse and/or diffuse-in-aggregates arrangements, and paratracheal, as vasicentric sheaths 1 or 2 cells wide. Sometimes a ladderlike configuration is formed on the transverse section by short bands of axial parenchyma which frequently intercept vascular rays (e.g., in *T. angustifolium*).

Storying of tissues occurs in the wood of *Theobroma*, but in its most highly developed state, it would have to be considered inconspicuous. Where it does appear, it is limited in distribution and confined to the uniseriate rays. In *T. microcarpum* it was also observed in the axial parenchyma.

Crystals occur in the wood of all species examined. Generally they are more frequent and conspicuous in the cells of rays, although they also occur in axial parenchyma cells of some species. In rays, only crystals of rhomboidal nature were observed except in *T. microcarpum* where large druses were present exclusively. Crystals in axial parenchyma cells are mostly rhomboidal, but in some species small druses occur.

DISCUSSION.—The most significant anatomical studies of the wood of Sterculiaceae are those of Chattaway (1932, 1933, 1937). Unfortunately, her work is of limited value as a basis for comparison here,

for she adopted the restricted view of the family proposed by Edlin (1935) and confined herself to the tribe Sterculieae. It should be mentioned that Edlin suggested dividing the Sterculiaceae, as treated by Bentham and Hooker (1862), into two families: Sterculiaceae, to be restricted to the tribe Sterculieae, and Buettneriaceae, to contain all other taxa (including *Theobroma*). Chattaway corroborated Edlin's proposals according to the anatomical findings which resulted from her studies. Nevertheless, it does not seem to me, judging solely from her summary of the characteristic anatomical features of the Sterculiaceae (*sensu stricto*), that the wood anatomy of *Theobroma* (which would be eliminated from Sterculiaceae according to Edlin's concept) would preclude its being allied with the species upon which she reported if we used only anatomical bases. There are only two apparent anatomical differences between *Theobroma* wood and that of Sterculiaceae (*sensu stricto*): Regardless of statements to the contrary (Metcalf and Chalk 1950, p. 251), the imperforate elements in *Theobroma* wood are not libriform wood fibers, but fiber-tracheids with small bordered pits (*sensu* Bailey 1936). Chattaway describes corresponding cells in Sterculiaceae (*sensu stricto*) as libriform wood fibers. Also, she indicates that the rays in *Theobroma* woods lack sheath cells (Chattaway 1932, 1937), "but are present in the rays of all genera of the Sterculiaceae except *Heritiera*." I cannot agree that *Theobroma* rays are totally devoid of these specialized elements. Although they are of sporadic occurrence, it is relatively easy to demonstrate them among the rays in any given tangential section.

In summary we can say that *Theobroma* woods are characterized by fiber-tracheids with small bordered pits, mostly solitary pores, simple perforation plates, alternate intervacular pitting, both homocellular uniseriate rays and heterocellular multiseriate rays with sheath cells in the same species, both apotracheal and paratracheal axial parenchyma in the same species, and crystalliferous deposits which are most abundant in the cells of ray tissue. Storied structure is present to a limited degree and is confined largely to the uniseriate rays. Although anatomy is variable within specimens of a given species, it is not consistently variable to allow for the division of the genus on anatomical grounds. In my opinion, the wood anatomy of *Theobroma* does not differ significantly from that in Edlin's Sterculiaceae as delineated by Chattaway.

Pollen Morphology of *Theobroma* and Related Genera

CONTRIBUTED BY G. ERDTMAN³

Theobroma L. (fig. 10): Pollen grains 3-colporate, peritreme, suboblate (about $15-22 \times 17.5-25 \mu$).

³ Palynological Laboratory of the Swedish Natural Science Research Council, Stockholm.

Species investigated: *T. angustifolium* Moc. & Sessé (*Pittier* s.n.): about $? \times 23.5 \mu$; *T. bernouillii* Pitt. (*Pittier* 4105): about $? \times 22 \mu$; *T. bicolor* Humb. & Bonpl. (*Klug* 2021): about $16 \times 18 \mu$; *T. cacao* L. (*Calderon* 107): about $15 \times 17.5 \mu$; *T. glaucum* Karst. (*Holliday & Cope* T-118): about $22 \times 24.5 \mu$; *T. grandiflorum* Schum. (*Archer* 7549): about $19 \times 22.5 \mu$; *T. microcarpum* Mart. (*Archer* 7551): about $16.5 \times 21 \mu$; *T. speciosum* Willd. var. *coriaceum* Huber (*Rusby* 647): about $22 \times 24.5 \mu$.

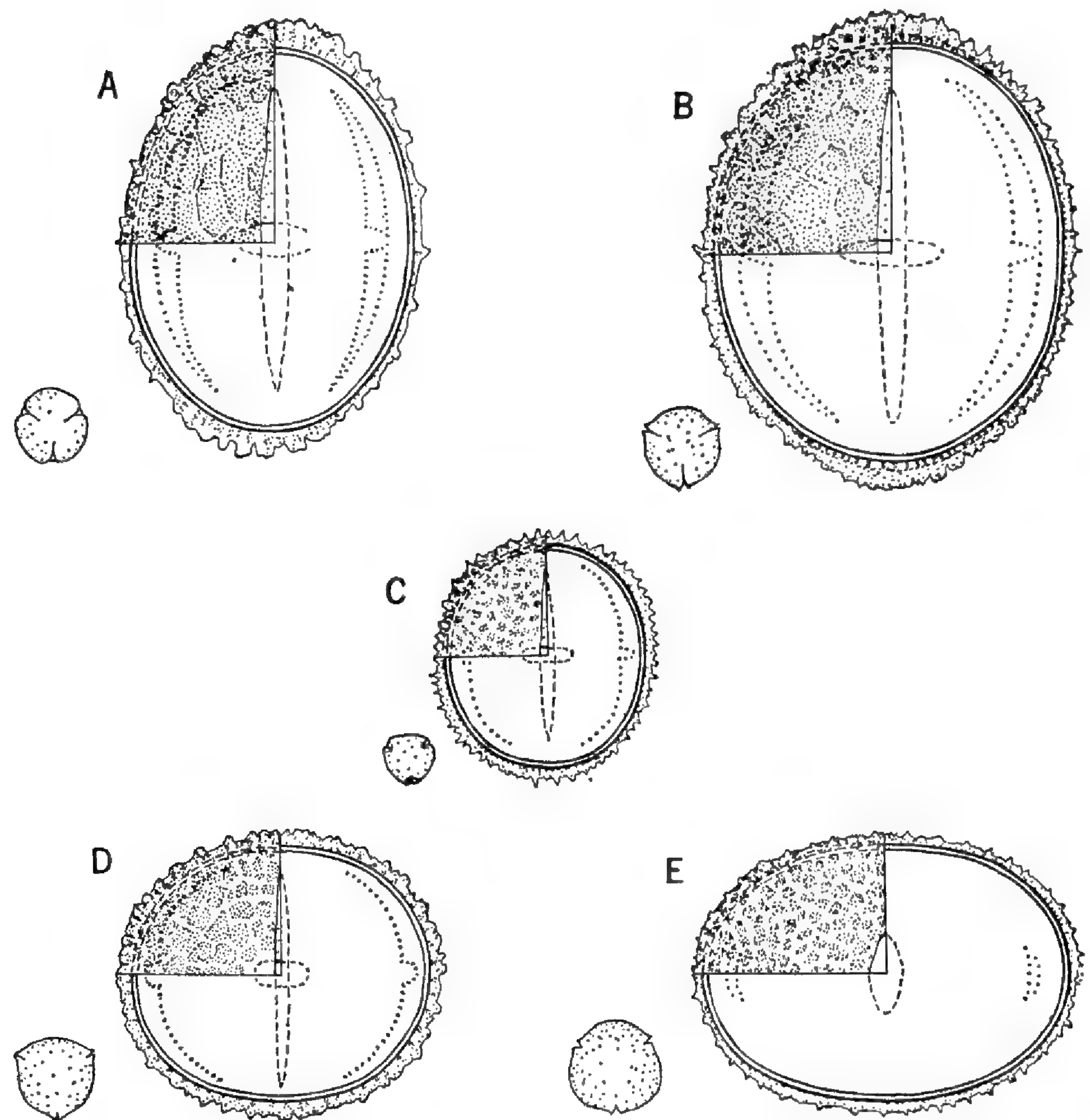


FIGURE 10.—Palynograms, $\times 1500$: A, *Herrania pulcherrima* v. *pacifica* Schult.; B, *Glossostemon bruguieri* DC.; C, *Guazuma polybotrya* Cav.; D, *Theobroma glaucum* Karst.; E, *Abroma augusta* L.; G. Erdtman & A. L. Nilsson, original.

Examples: *T. glaucum* Karst. (*Holliday & Cope* T-118): pollen grains 3-colporate, peritreme (amb circular), oblate spheroidal (about $22 \times 24.5 \mu$). Apocolpium diameter about 18μ . Colpi narrow, about 18μ long. Ora about 3.5μ broad. Exine about 1.5μ thick. Sexine as thick as nexine or slightly thicker, tectate. Tegillum distinctly undulating. The waves of the tegillum are smoother than those of, for example, *Herrania pulcherrima* var. *pacifica*, but nevertheless they impart to the pollen surface a reticuloid pattern with muroid ridges (supported by one or two rows of endosexinous bacula) separated by luminoid depressions (diameter up to 3μ). The tegillar bottom of the latter seems to be supported by stray baculoid rods.

T. microcarpum Mart. (*Archer* 7551): pollen grains 3-colporate (amb circular), suboblate (about $16.5 \times 21 \mu$). Apocolpium diameter about 13.5μ . Colpi narrow, about 10μ long. Ora lalongate (about $1.5 \times 3 \mu$). Exine about 1.6μ thick. Sexine thicker than nexine, tectate, undulating (waves not as smooth as in *T. glaucum*). Reticuloid pattern much as in *T. glaucum*, with more or less irregular luminoid areas (longest axis up to about 3.5μ).

T. speciosum Willd. var. *coriaceum* Huber (*Rusby* 647): pollen grains 3-colporate, oblate spheroidal (about $22 \times 24.5 \mu$). A single 4-colporate (loxocolpate) pollen grain seen.

Apocolpium diameter about 15μ . Colpi narrow, about 12μ long. Ora lalongate (about $3 \times 8 \mu$).

Exine about 1.5μ thick or a little less. Sexine thicker than nexine, probably tectate, presenting a reticuloid pattern (OL) with narrow straight muroid and irregularly polygonal luminoid areas (maximum diameter of the latter 1.5μ). Muroid areas supported by a single row of endosexinous bacula.

The pollen grains of *Herrania* differ from those of *Theobroma*.

Herrania Goud.: pollen grains 3-colporate, peritreme, prolate (about $32-35 \times 23-25 \mu$).

Species investigated: *H. camargoana* Schult. (*Baker* 39): about $34 \times 25 \mu$; *H. cuatrecasana* Garcia B. (*Cuatrecasas* 11168): about $35 \times 24 \mu$; *H. mariae* Schum. (*Ducke* 595 and *Martius* 318 (type)): about $33 \times 25 \mu$; *H. pulcherrima* var. *pacifica* Schult. (*Patiño* 23): about $32 \times 23 \mu$.

Example: *H. pulcherrima* var. *pacifica* Schult.: pollen grains 3-colporate, peritreme, prolate (about $32 \times 23 \mu$).

Apocolpium diameter about 14μ . Colpi about 25μ . Ora about 2.25μ high, slightly lalongate, their horizontal margins incrassate.

Exine about 2μ thick at poles, 1μ at center of mesocolpia. Sexine thicker than nexine, tectate. Tegillum undulating, with anastomos-

ing, slightly winding, crestlike and slightly carinate folds imparting a distinct reticuloid LO-pattern to the exine surface. Crests about $1\ \mu$ broad at the poles, gradually more narrow (about $0.5\ \mu$ or less) in mesocolpia. They are supported by a single row of endosexinous bacula except at the poles, where there are several rows. The luminoid, concave areas between the folds of the tegillum are equally supported by small endosexinous bacula or baculoid rods (largest and longest at the poles). The longest diameter of these areas varies between 2 and $5\ \mu$ or more.

The pollen grains in *Glossostemon bruguieri* are somewhat similar to those in *Herrania*.

Glossostemon bruguieri DC. (Iraq, Falluja, Haines s.n.): pollen grains 3-colporate, peritreme, subprolate ($35 \times 28\ \mu$).

Apocolpium diameter about $8\ \mu$. Colpi about $25\ \mu$, constricted at the equator, ends rounded, margins thickened. Ora lalongate (about $8 \times 1.5\ \mu$).

Exine about $2.1\ \mu$ thick at the poles, about $1\ \mu$ at the equator. Sexine thicker than nexine, tectate. Tegillum strongly undulating, forming distinct, anastomosing muroid ridges (about $0.5\ \mu$ wide) separated by luminoid areas. In the apocolpia and towards the colpi margins the latter are very small (diameter usually not exceeding $0.5\ \mu$); in the mesocolpia they are larger (longest diameter up to $4\ \mu$). The muroid ridges are supported by a single or double row of endosexinous bacula. The tegillar bottom of the luminoid areas is also supported by small bacula. Bacula in apocolpia considerably longer than those in mesocolpia.

The pollen grains in *Abroma* and *Guazuma* are somewhat similar to those in *Theobroma*.

Examples: *Abroma augusta* L. (Assam; herb. Riksmus., Stockholm, marked "no. 370"): pollen grains cf. 3-colporate, peritreme, oblate ($21 \times 29\ \mu$).

Apocolpium diameter about $23\ \mu$. Colpi about $5.5 \times 2.5\ \mu$, their margins incrassate. Ora not very distinct.

Exine about $1\ \mu$ thick, tectate, very slightly undulating, presenting a reticuloid pattern. Muroid ridges low, about $1\ \mu$ wide, supported by a double row of endosexinous bacula and enclosing small rounded luminoid areas 1 – $2\ \mu$ wide. Under each of the latter is one or several endosexinous bacula.

Guazuma polybothra Cav. (Cuba, Boldo s.n.; herb. Madrid, marked "no. 94"): pollen grains 3-colporate, peritreme, prolate spheroidal ($18.5 \times 16.5\ \mu$).

Apocolpium diameter about $12\ \mu$. Colpi about $12\ \mu$ long.

Exine about $1\ \mu$ thick, tectate, undulating, with distinct narrow,

carinate muroid folds separated by luminoid, concave areas (diameter less than $1\ \mu$ in apocolpia as well as in mesocolpia).

Guazuma ulmifolia Lam. (Mexico, *Pringle* 2570): pollen grains 3-colporate, peritreme, spheroidal (16μ).

Apocolpium diameter about $5\ \mu$. Colpi about $14\ \mu$ long, $1\ \mu$ wide. Ora lalongate, about $1\ \mu$ high and $3.5\ \mu$ wide.

Exine about $1\ \mu$ thick (of the same thickness in apocolpia as in mesocolpia, probably tectate (tegillum undulating, exhibiting narrow, muroid ridges separated by luminoid areas less than $1\ \mu$ in diameter).

Cytology ⁴

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CHROMOSOME NUMBERS IN THEOBROMA SPECIES.—The first published count of $2n=20$ for *T. cacao*, the now accepted figure, was made by Davie (1933) from studies of mitosis in root-tips. He noted that "the chromosomes are very small, quite different from Malvaceous chromosomes. A few show median constrictions. Two pairs of satellited chromosomes were seen." In 1935, Davie confirmed the diploid number of 20 from studies of meiosis in pollen mother cells of *T. cacao*.

Confirmation of this number has been made for *T. cacao* by Carletto (1946), Muñoz Ortega (1948), Simmonds (1954) and Cope (unpublished). The first three authors have also shown twenty to be the diploid number in other *Theobroma* species. Carletto counted 20 chromosomes in *T. "leiocarpa," T. speciosum*, and *T. grandiflorum* and Muñoz Ortega in *T. "leiocarpa," T. "pentagona," T. bicolor*, *T. microcarpum*, *T. speciosum*, *T. simiarum*, *T. capilliferum*, *T. grandiflorum*, *T. obovatum*, *T. angustifolium* and *T. cirmolinae*. Simmonds confirmed $2n=20$ in *T. bicolor* and *T. angustifolium*. According to Muñoz Ortega, the chromosomes throughout the genus show medial, submedial, and terminal centromeres. The chromosomes are uniformly small, with size gradations within each species examined. The largest chromosomes of *T. cacao* are $2\ \mu$ in length; the smallest of *T. microcarpum* only $0.5\ \mu$ long.

⁴ REFERENCES:

- Carletto, G. M. (1946). O numero de cromosômos em cacaueiros. Bol. Tec. Inst. Cacau Bahia No. 6, 35-39.
 Davie, J. H. (1933). Cytological studies in the Malvaceae and related families. Journ. Genet. 28: 33-67.
 Davie, J. H. (1935). Chromosome studies in the Malvaceae and certain related families II. Genetica, 17: 487-498.
 Muñoz Ortega, J. M. (1948). Estudios cromosómicos en el género *Theobroma* L. MSS in library of the Instituto Interamericano de Ciencias Agrícolas, Turrialba, Costa Rica.
 Simmonds, N. W. (1954). Chromosome behavior in some tropical plants. Heredity, 8: 139-146.

Pollen Incompatibility ⁵

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The incidence of self- and cross-incompatibility, and self- and cross-compatibility in *T. cacao* was first discovered by Pound (1932) when he showed that some trees in Trinidad could not set fruit with their own pollen nor with one another's. These self- and cross-incompatible trees needed pollen from a self-compatible tree in order to set fruit. Posnette (1945) discovered cross-compatibility between self-incompatible types in his studies on cacao trees introduced from the upper Amazon into Trinidad. The existence of self-incompatible and self-compatible cacao trees has now been established in nearly all areas where the species is wild or cultivated.

Cope has shown, in a series of publications, that unlike most other plant species showing incompatibility the site of the incompatibility reaction in cacao is in the embryo-sac, and not in the stigma or in the style. Pollen tubes in incompatible pollinations grow as fast as those in compatible pollinations and deliver their male gametes into the embryo-sacs in perfectly normal fashion. It is only when the male gametes come to lie in contact with their female counterparts that any abnormality appears (fig. 11). According to the genotype of the tree or trees involved in an incompatible pollination, either one quarter, one half, or all encounters between male and female gametes result in failure of the fusion process. When an incompatibly pollinated cacao flower falls from the tree 25%, 50%, or 100% of the ovules in the ovary show nonfusion; in the first two cases the other fertilized ovules in the same ovary show normal fusion between the gametes to give a zygote and a triploid primary endosperm nucleus in each.

The genetic system controlling the nonfusion and fusion of gametes in the embryo-sac of *T. cacao* is now known. Three complementary loci appear to be involved, which have been called A, B, and S. The first two show simple dominance and recessivity; the S locus carries multiple alleles between which dominance and independence relationships exist. The action of the S locus was first postulated by Knight and Rogers (1955), based on results obtained from wholly self-incompatible material. The need for other loci, to act in a complementary

⁵ REFERENCES:

- Cope, F. W. (1939). Studies in the mechanism of self-incompatibility in cacao I. 8th Ann. Rep. on Cacao Res. (1939), Trinidad, 20, 21.
———(1940). Studies in the mechanism of self-incompatibility in cacao II. 9th Ann. Rep. on Cacao Res. (1939), Trinidad, 19-23.
———(1958). Incompatibility in *Theobroma cacao*. Nature, London, 181, 279.
———(1959). Incompatibility in *Theobroma cacao*. A Rep. on Cacao Res., 1957-58, 7-17.
Knight, R., and Rogers, H. H. (1955). Incompatibility in *Theobroma cacao*. Heredity, 9: 69-77.
Posnette, A. F. (1945). Incompatibility in Amazon cacao. Trop. Agriculture, Trin., 22: 184-187.
Pound, F. J. (1932). Studies in fruitfulness in cacao. II—Evidence for partial sterility. 1st Ann. Rep. on Cacao Res. (1931), Trinidad, 24, 25.

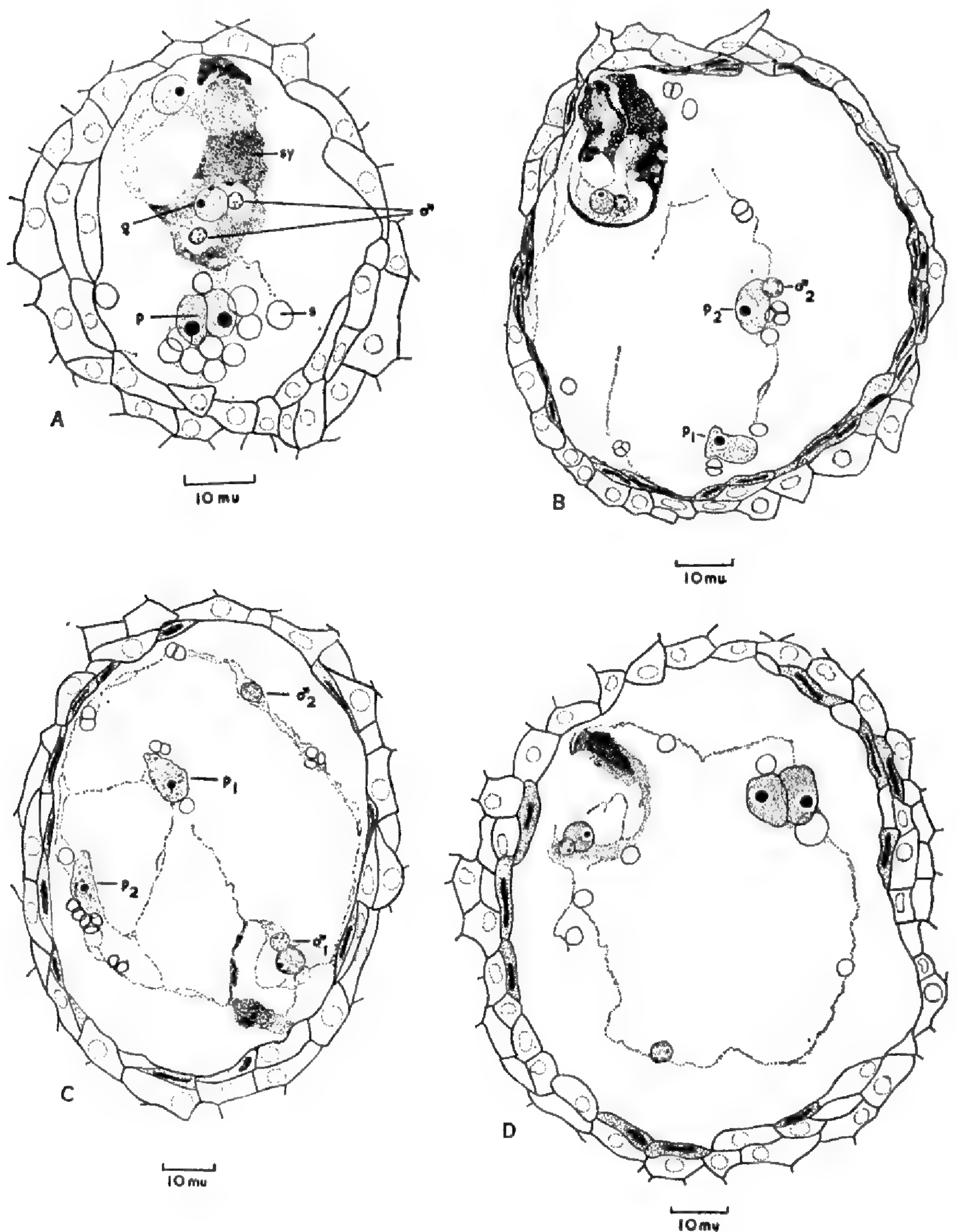


FIGURE 11.—A, Camera lucida drawing of an embryo sac of *Theobroma cacao*, fixed 24 hours after pollination: one male gamete (σ^1) is in contact with the egg nucleus (φ) and the second is moving towards the polar nuclei, p; the darkly-staining synergid cell (sy) has been penetrated by the pollen tube; and starch grains (s) are abundant. B, camera lucida drawing of an incompatibility fertilized embryo sac of *T. cacao*, 72 hours after pollination: one male nucleus lies in contact with the egg nucleus (top L.H.); and the second male nucleus (σ^2) is associated, unfused, with one polar nucleus (p_2), the other polar (p_1) having moved away. C, as in B, except that the second male nucleus (σ^2) and the two polar nuclei (p_1 and p_2) are all dissociated (σ^1 is the first male gamete lying in contact with the egg nucleus). D, as in B, except that the second male nucleus is separated from the two coherent polar nuclei. F.W. Cope, original.

manner with the S locus, was pointed out by Cope (1958) in order to explain the emergence of self-incompatible progeny from a cross between two true-breeding self-compatible parents.

The A and B loci both act before meiosis. When both are at least heterozygous for the dominant allele, it is believed that a general precursor substance is produced and on this the S locus acts to produce very highly specific incompatibility reactions between gametes carrying the same S allele. The S locus acts both before and after meiosis, the premeiotic action giving the overall sporophytic control of incompatibility and the postmeiotic action leading to a gametophytic reaction between gametes.

If one or more of the A, B, and S loci become homozygous for an inactive allele the self-incompatible condition is lost; the tree is then self-compatible and cross-compatible with any other cacao genotype.

A few examples of genotypes of the two classes of tree are:

Self-incompatible

AABBS_{x,y}

AaBbS_{x,y}

AABbS_{x,x}

AaBBS_{x,i}

Self-compatible

aaBBS_{x,y}

aaBBS_{x,i}

aabbS_{x,x}

AABBS_{i,i}

aaBbS_{i,i}

where S_x and S_y are two active S alleles and S_i is an inactive amorph of the S series.

Self-incompatible genotypes are also cross-incompatible if they have common dominant S alleles; if one has alleles independent in action and one of these is duplicated in the other as a dominant; or if both genotypes, carrying only alleles of independent action, have one allele in common.

Genus *Theobroma* ⁶ L.

Theobroma L. [Gen. Pl. 351. 1737; Hort. Cliff. 379. 1737] Sp. Pl. 782. 1753; Gen. Pl. ed. 5, 340. 1754; Benth. & Hook. (1862) 225; Bernoulli (1869) 4; Schumann (1890) 86 *pro parte*; Schumann (1896) *pro parte*; Chevalier (1946) 269.

Cacao [Tourn. Inst. 660, t. 444. 1700]. Miller, Gard. Dict. Abr. ed. 4th. 1754. *Tribroma* Cook, Journ. Washington Acad. Sci. 5:288. 1915.

TYPE.—*Theobroma cacao* L.

Flowers hermaphroditic, pentamerous, pentacyclic, diplostemonous. Buds globose, ovoid or oblong-ovoid. Sepals 5, valvate in aestivation, almost free and spreading or more or less united in the lower part, cupular, or united by pairs into one single and two double lobes, or rarely in two lobes. Petals 5, dextrorsely contorted in aestivation, each one strangulated in two halves: 1) a lower part corresponding

⁶ *Theobroma* is a neuter name and the genus must be neuter by the present International Code of Nomenclature. The feminine endings for the species used by some authors (De Candolle, Bernoulli, Chevalier, etc.) are corrected in this revision into the neuter form except for the original bibliographic references.

to the claw, rigid and strongly veined with the shape of a hood (cucullus); 2) an upper part, a flat blade (lamina), articulated to the inflexed apex of the claw. Androecium in two verticils of five, united in a tube at base: an outer whorl with 5 sterile, petaloid or linear staminodes, opposite to the sepals; an inner whorl with 5 fertile stamens opposite to the petals, the filaments short, minutely 2-3-branched, each branch with an anther. Anthers hidden inside the petal-hoods, bilobate (bithecate), the thecae unilocular and dehiscent by longitudinal clefts. Pollen grains 3-colporate, peritreme, suboblate (about $15-22 \times 17.5-25 \mu$). Gynoecium 5-carpellar, syncarpic, superior, the carpels opposite to petals, the ovary ovoid, pentagonal, 5-celled with axile placentation, the many ovules in two rows in each cell. Stylodes 5, connivent, free or more or less united, filiform. Stigmas apical, short, acute. Ovules anatropous with two integuments and dorsal raphe.

Fruit large, subbaccate or subdrupaceous, indehiscent, ovoid, ellipsoid or oblong, obtuse or acute, smooth or ridged, rugose or tuberculate, the pericarp fleshy or hard and partly woody or coriaceous, the vascular axis thin and vanishing; seeds usually in five rows, each one surrounded by a thick, fibrose, pulpy tissue filling the cavity at maturity, ovoid, ellipsoid, or amygdaloid, the episperm double, thick, subcoriaceous, the outer layer with a trichomatic and gelatinous epiderm developing into a thick, pulpy envelope; embryo straight, the radicle cylindrical, inferior; cotyledons thick, strongly plicate-corrugate; endosperm usually reduced to a filmy membrane covering the cotyledons. Germination epigeous or hypogeous.

Evergreen tree with the apical growth of the stem limited to the production of a terminal whorl of 3-5 spreading branches; sympodial growth of the stem attained by adventitious upright subterminal shoots or by pseudoapical shoots from buds axillary to the apical branching whorl. Primary branching of stem 3- or 5-verticillate, the further branching alternate. Leaves simple, entire, penninerved, persistent, coriaceous, long-petiolate and varied in phyllotaxy on the primary stems, short-petiolate and distichous on the branches.

Inflorescences dichasial or monochasial (cincinnate), axillary or on reduced tuberculiform branchlets on trunk and larger branches. Peduncles bracteate, articulate to pedicels.

Pluricellular trichomes in all species, usually as stellate hairs, rarely simple. Globose, stipitate glands present in some species.

Chromosome number: $2n=20$.

Subgeneric classification

The division of the genus *Theobroma* in five sections by Bernoulli is the best to date. He used the characters of the petal-lamina (sessile, stipitate, or lacking), shape of staminodes and their position

in the bud, and the number of anthers. A sound combination of these characters gives five very natural groups. Schumann's (1886, 1890) separation of two sections, *Theobroma* and *Bubroma*, according to their 2-antheriferous or 3-antheriferous stamens, leads to an unnatural grouping because the number of anthers for each stamen may vary in the same section and even in the same species (e.g., *T. glaucum*). For this reason, the combination of Schumann's with Bernoulli's classification made by Pittier (1930) was erroneous, because the section *Oreanthes* cannot be placed in either of Schumann's two groups. Chevalier (1946) used both classifications but without trying to integrate them. Ducke (1954), who published the best elaborated key for 7 Brazilian species, did not pay attention to sections, but he used the 3- or 5-whorled branching as a new character to distinguish the species. Another character, the epigeous or hypogeous germination of the seeds correlated with growth-habit of the tree, was used by Addison and Tavares (1951) for distinguishing species, and by Cope and Bartley (1960) in classifying them.

I have applied to the classification the mode of germination, and the growth and the branching system for all the species, and I have found the sections founded by Bernoulli to be very much reinforced by the addition of these vegetative features, and other floral and fruit characters unknown before. Epigeous germination and subterminal growth apply to all species of the sections *Rhytidocarpus*, *Oreanthes*, and *Theobroma*, whereas the other sections exhibit hypogeous germination and pseudoterminal growing. These vegetative characters prove to be very important and basic, being uniform for each section, but like other characters, even though constant within the section, they are not sufficient to give taxonomic recognition to the two groups separated by those characters. The Bernoulli sections are all of similar rank, independent and probably of parallel origin. Only the new section *Andropetalum*, based in its extraordinarily broad and reflexed staminodes, relatively reduced petal-lamina, and gamosepalous calyx, seems to be closer to *Glossopetalum* than the other sections to each other. The fruit structure, as explained above, is also important in the present classification. The following key will give a clear idea of the characters of each section. Another artificial key is added to facilitate the identification of specimens lacking complete information.

The position of the inflorescences (cauline or axillary), the color, size, and shape of petal-lamina and staminodes, number of anthers, shape of sepals and indument, form and size of fruits, the outline, venation, thickness, and firmness of leaves, and especially the kind of indumentum they bear, as well as the pilosity on different parts of the flowers, inflorescences, and branchlets, and the form and caducousness of stipules are the characters used to distinguish the species.

Key to Sections of *Theobroma*

1. Cotyledons epigeous at germination; growth of stem by adventitious upright, lateral-subterminal shoots; staminodes in aestivation erect.
2. Staminodes thick-linear, obtuse; petal-hood 1-nerved; petal-lamina subsessile; stamens 2-antheriferous; pericarp thick, ridged and nerved, the mesocarp very hard, woody; primary branches ternate; leaves tomentose beneath 1. **Rhytidocarpus**
(Contains the single species: *T. bicolor*)
2. Staminodes linear-subulate or lanceolate, acute; petal-hood 3-nerved.
3. Petal-lamina sessile; stamens 3- or 2-antheriferous; pericarp coriaceous; primary branches ternate; leaves tomentose beneath . . . 2. **Oreanthes**
3. Petal-lamina attenuate-stipitate; stamens 2-antheriferous; pericarp firmly carnose; primary branches quinate; leaves glabrous or puberulous beneath 3. **Theobroma**
(Contains the single species: *T. cacao*)
1. Cotyledons hypogeous at germination; growth of stem pseudoapical; primary branches ternate; stamens 3-antheriferous.
4. Staminodes flexuose in bud, ovate, subulate-caudate; petal-hood 5-nerved; petal-lamina lacking; pericarp carnose-coriaceous, lignose-ridged and reticulate; leaves glabrous or puberulous 4. **Telmatocarpus**
4. Staminodes reflexed in bud, obovate-oblong, broadly lanceolate or broadly obovate, reflexed or erect in anthesis; petal-hood 7-nerved; pericarp rigid, the epicarp hard, woody; leaves tomentose beneath.
5. Staminodes oblong-obovate or lanceolate, reflexed or erect at anthesis; petal-lamina broadly developed, flat, stipitate; sepals more or less united and reflexed 5. **Glossopetalum**
5. Staminodes broadly obovate, as broad as long; petal-lamina somewhat reduced, narrow, and plicate; calyx cupular, the sepals united one half or one third their length 6. **Andropetalum**
(Contains the single species: *T. mammosum*)

KEY TO SECTION OREANTHES

1. Leaves stellate-tomentose beneath on the minor reticulate veins, the areoles densely, minutely, stellulate-tomentose.
2. Filaments 2-antheriferous; inflorescences small, on the leafy branches; flowers rather small (sepals 7-9 x 2-2.5 mm.); fruits globose-elliptical about 10 x 9 cm., glaucous when ripe. Leaves beneath with the quaternary nerves, minor veins, and areoles covered by minute tomentum of minute, thin, white, stellate hairs 2. **T. sylvestre**
2. Filaments 3-antheriferous; inflorescences on the trunk, multiflorous; flowers rather large (sepals 10-12 x 3.5-4 mm.).
3. Leaves with glabrous primary and secondary nerves beneath or subglabrous with very scattered mediocre stellate hairs and sparse callose spots; fruit globose-ellipsoid, 10 x 8 cm., without ribs, shortly tomentose, yellowish when ripe 3. **T. speciosum**
3. Leaves softly velutinous beneath, the nerves and veins with abundant long, thin, patulous stellate hairs; fruits ellipsoid, densely velutinous, with 5 very prominent ribs 4. **T. velutinum**
1. Leaves with glabrous nerves and veins beneath, or subglabrous with very sparse, mediocre stellate hairs, only the areoles covered with compact tomentum of minute, white, stellate hairs.

4. Flowers large: petal-lamina suborbicular 5.5–7 x 5–6.5 mm.; petal-hood 5–6 x 2.5–3 mm.; staminodes lanceolate-subulate 10–12 mm. long; filaments 2–3-antheriferous; sepals 12–13 x 3–4 mm.; petal-hood puberulous; fruit ellipsoid, obtusely pentagonal, attenuate at apex, umbilicate at base, 10–11 x 5–5.5 cm. Leaves coriaceous, broadly ovate or ovate-oblong.

5. *T. glaucum*

4. Flowers smaller: petal-lamina suborbicular, orbicular or elliptic, 2.5–4 mm. long; staminodes 6–9 mm. long; filaments 2-antheriferous; sepals 8–10 x 3 mm.; petal-hood hirtellous pubescent; fruit ellipsoid-oblong, obtusely pentagonal, abruptly narrowed at apex, umbilicate at base, constricted or not above the base, 12–25 x 5.2–8 cm. 6. *T. bernouillii*

KEY TO SECTION TELMATOCARPUS

1. Leaves regularly penninerved; inflorescences on trunk and branches; peduncles 5–25 mm. long; pedicels 7–8 mm. long; fruit peduncles 2–3 cm. long; sepals stellate-tomentose; petals pilose above, narrowed in the lower third, the apex blunt or emarginate; staminode-base with very short, thick hairs; ovary ovoid-ellipsoid, tomentose; fruit, when ripe, ovoid, attenuate at apex, slightly 5-costate, alveolate, the epicarp densely appressed tomentose, 7.5–11 x 7–9 cm. 8. *T. gileri*
1. Leaves at base 3-nerved, the two lateral basal nerves ascending at an acute angle, the other 2 or 3 pairs of secondary nerves remotely higher; inflorescences axillary on young branchlets; peduncles 0.5–1 mm. long; pedicels 0.5–1 mm. long; fruiting peduncles 4–8 mm. long and thick; sepals with sparse stellate hairs; petals glabrous, gradually attenuate to the base, the apex acuminate, the acumen acute, 2-dentate; staminode-base with rather thick, long, flexuose hairs; ovary pyriform, glabrous or sparsely granulate, rarely sparsely stellate-pilose; fruit, when ripe, ellipsoid-globose, conspicuously 10-costate, reticulate-alveolate, usually 6.5–7 x 6–6.5 cm. 9. *T. microcarpum*

KEY TO SECTION GLOSSOPETALUM

1. Inflorescences born on the trunk and main branches. Flowers large; staminodes obovate-oblong or oblong-spathulate, 9–11 mm. long, erect in anthesis; leaves large (20–54 x 8–30 cm.), coriaceous, obtuse at both ends, strongly nerved and tomentose beneath; stipules coriaceous, persistent; calyx 5-lobate, cupular at base reflexed.
2. Petal-lamina and staminodes yellow.
3. Fruit ellipsoid-oblong or ovoid-oblong, attenuate at both ends, umbilicate, obtusely pentagonal, 25–35 x 10–12 cm.; leaves oblong-elliptic or ovate-elliptic, subvelvety beneath with minute, stellate, flexuose, white hairs crowded on the areoles and minor veins, and other equal or slightly larger hairs on the other nerves; stipules oblong-lanceolate, subacute; petal-lamina subdeltoid-spatulate; staminodes oblong-obovate. 11. *T. cirmolinae*
3. Fruit ovoid-ellipsoid or ellipsoid, smooth, rounded at both ends or slightly attenuate at apex, 18–22 x 9–11 cm.; leaves oblong-elliptic or ovate-elliptic, tomentose beneath with minute, stellate, flexuose, white hairs crowded on the areoles and minor veins, and other larger, thicker, ferruginous hairs copious on the other nerves; stipules ovate or ovate-oblong, obtuse; petal-lamina subtriangular-spatulate; staminodes oblong-obovate 12. *T. stipulatum*

2. Petal-lamina and staminodes red. Fruits smooth (not ridged).

4. Fruit ellipsoid-oblong, rounded at apex, umbilicate, 16-40 x 6-11 cm.; leaves obovate-oblong, densely covered beneath with minute, stellate, white, intricate hairs on the areoles and minor veins, other mediocre, stellate, ferruginous hairs sparse or copious on nerves, and larger ones with longer rays usually copious on the major nerves; stipules lanceolate; petal-lamina subtrapezoid, attenuate at base; staminodes oblong-obovate 14. **T. simiarum**

4. Fruit ellipsoid-ovoid, rounded at base, obtuse at apex, 19-20 x 10-11.5 cm.; leaves oblong-elliptic or ovate, often rugose, densely covered beneath with minute, stellate, white, intricate hairs on areoles and minor veins, and other larger ferruginous hairs with longer, spreading rays abundant on nerves; stipules ovate, rather obtuse; petal-lamina obovate-deltoid, attenuate at base; staminodes obovate-oblong.

13. **T. chocoense**

1. Inflorescences small, axillary on foliose branches.

5. Petal-lamina and staminodes yellow; staminodes oblong-obovate, erect. Calyx trilobate, reflexed; leaves thin, subcoriaceous, subobovate-oblong or elliptic-oblong (9-25 x 3-9 cm.), attenuate at both ends, acute, cinereous beneath with minute, stellate, whitish, intricate hairs and larger ones with longer, patulous rays on nerves; stipules membranaceous, subulate, deciduous; petal-lamina subobovate-spatulate, bilobate, emarginate; fruit ellipsoid-elongate, 5-angulate, more or less irregularly tuberculate, 10-18 x 6-9 cm. 10. **T. angustifolium**

5. Petal-lamina and staminodes red; staminodes curved, spreading in anthesis.

6. Young branchlets, petioles, and buds covered with a woolly-floccose, ochraceous or tawny, deciduous tomentum. Adult leaves glaucous or glauco-cinereous, monotrichous beneath, with the principal and tertiary nerves glabrous, glossy, reddish punctate, the areoles and reticulum whitish tomentose by minute stellate hairs.

7. Flowers large; calyx (14-15 mm. long) 3-lobate; staminodes very acute, lanceolate, spreading (9-13 mm. long); petal-lamina trapezoid-elliptic, thick, dark red; leaves firm-coriaceous; stipules subcoriaceous, persistent; fruits ellipsoid, 16-25 x 10-12 cm., rounded at both ends, smooth 15. **T. grandiflorum**

7. Flowers smaller; calyx (about 7 mm. long) 5-parted; staminodes oblong-elliptic, rounded at apex (6 x 2.8-3 mm.); petal-lamina suborbicular, red, rather thick; leaves thin-chartaceous, very asymmetrical at base; stipules membranaceous, linear-subulate, deciduous; fruit ellipsoid-obovoid, acute, granulate-tuberculate, 5-7 x 3-4 cm.

16. **T. obovatum**

6. Young branchlets, buds and petioles hirsute, or short-tomentose. Calyx 5-parted.

8. Young branchlets, buds, and petioles densely hirsute or hirsute-tomentose; leaves beneath tomentose-hirsute (especially in young plants), ferruginous or ochraceous by spreading long-radiate hairs on the nerves and veins, and with minute, white, intricate ones covering the surface.

9. Pedicels 5-10 mm. long; peduncles 5-10 mm. long; inflorescences loose; sepals about 10 mm. long; petal-lamina and staminodes not ciliate; fruit ellipsoid-pyriform, smooth 20. **T. sinuosum**

9. Pedicels up to 1 mm. long; peduncles up to 6 mm. long; inflorescences compact, glomerate; sepals about 7 mm. long; petal-lamina and staminodes ciliate; fruit unknown 21. **T. canumanense**
8. Young branchlets, buds, and petioles densely subappressed-tomentose; leaves cinereous or ferruginous beneath with minute, stellate, whitish, intricate hairs covering the areoles and the smallest reticulum and mediocre, thicker, ferruginous hairs, copious or scattered on the nerves.
10. Bracteoles narrowly linear.
11. Staminodes scarlet, lanceolate, acute or subacute, 6–7.5 x 2 mm.; petal-lamina scarlet, orbicular or subrounded, thick, 2–2.5 x 2.2–3 mm.; ovary glabrous and smooth or very sparsely granular; fruit ellipsoid or oblong-ellipsoid, often slightly attenuate at base, 7.5–11.5 x 5–6.6 cm., the pericarp tomentose, smooth, 3–4 mm. thick when dry 17. **T. subincanum**
11. Staminodes brownish red, obovate-oblong, rounded or subspatulate at apex, 5–5.5 x 2–3 mm.; petal-lamina obovate-subrhombic, 4–5 x 4 mm.; ovary densely tomentose; fruit ellipsoid, rounded both ends, 7 x 4 cm. 18. **T. hylaeum**
10. Bracteoles 3, orbicular, cochlear, embracing the single bud; staminodes brownish red, obovate-oblong, rounded at apex, 6–7.5 x 3.5–4.5 mm.; petal-lamina oblong-elliptic or oblong-obovate, 5–7 x 3–5 mm.; ovary densely tomentose; fruit ellipsoid, rounded at apex, constricted above the base, 8–10 x 4.5–6 cm., the pericarp, when dry, 1–1.8 mm. thick, the epicarp 1 mm. thick, fragile at maturity 19. **T. nemorale**

Artificial key to the species

1. Leaves glabrous or puberulous beneath.
2. Leaves firmly coriaceous, regularly penninerved, with 10–14 secondary nerves each side, usually 20–30 x 7–10 cm.; fruits glabrous, ovate-oblong, more or less pentagonal or decagonal, with carnose relatively thick pericarp; stamens 2-antheriferous; staminodes linear-subulate, erect in bud, red; petal-lamina spatulate, stipitate, yellowish; jorquette with 5 branches; growth below jorquette. Flowers on trunk and on branchlets. 7. **T. cacao**
2. Leaves chartaceous with 3–6 pairs of secondary nerves; fruits smaller, ovoid or subglobose, with hard-costate reticulate tomentose pericarp; stamens 3-antheriferous; staminodes subulate-subflagelliform, flexuous in bud; petals lacking laminae or ligular appendages; jorquette with 3 branches; growth above jorquette.
3. Leaves 5–20 x 1.5–8 cm., regularly penninerved with 5 or 6 nerves on each side, puberulous beneath, the midrib tomentulose; peduncle 5–25 mm. long; pedicels 7–8 mm. long; ovary tomentose; fruit ovoid, slightly 5-costate and reticulate, 7.5–11 x 7–9 cm., fruiting peduncle 2–3 cm.; flowers on trunk and on branchlets. Sepals tomentulose. 8. **T. gileri**
3. Leaves 6–16 x 2–7 cm., 3-nerved at base, the two lateral-basal nerves ascending, quite distant from the other 2 or 3 pairs of secondary nerves, glabrous or minutely and sparsely puberulous beneath; peduncle 0.5–1 mm. long; pedicel 0.5–1 mm. long; ovary glabrous or sparsely granulate; fruit ellipsoid or subglobose ellipsoid, strongly

- 10-costate and reticulate 6.5–7 (–9) x 6–6.5 cm.; fruiting peduncle 4–8 mm. long; flowers only on branchlets . . . 9. **T. microcarpum**
1. Leaves densely stellate-tomentose beneath. Jorquette 3-branched.
 4. Leaves thin, chartaceous, tomentose-cinereous beneath. Flowers on terminal, leafy branchlets.
 5. Leaves ovate or ovate-oblong, subcordate or cordate at base, cinereous or ochraceo-cinereous (more or less silvery) beneath, the hairs uniform, minute, stellate, covering the surface and nerves; stamens 2-antheriferous; petal-lamina subsessile; growth below jorquette. Dichotomous inflorescences on branches; fruit large, ellipsoid with thick-woody, strongly costate-reticulate and lacunose pericarp; flowers small, red dish; staminodes thick-linear, obtuse 1. **T. bicolor**
 5. Leaves oblong, elliptic-oblong, lanceolate-oblong, regularly pinnate-nerved, obtuse or cuneate at base, tomentose-cinereous beneath; stamens 3-antheriferous; petal-lamina stipitate; growth above jorquette.
 6. Leaves obovate-elliptic or obovate-oblong, obtuse and very asymmetrical at base with 5–7 nerves each side, 7–35 x 3–13 cm.; homotrichous, covered by minute, dense, white, stellate hairs beneath, except for the glabrous red-punctate main veins; young vegetative parts with a floccose, lanate, ochraceous, deciduous indument; fruit small, ellipsoid-obovoid, tuberculate-warty, 5–7 x 3–4 cm.; calyx 5-lobate. Flowers small; staminodes petaloid, red.
16. **T. obovatum**
 6. Leaves elliptic-lanceolate or oblanceolate, rather oblong, slightly asymmetrical at base, heterotrichous beneath with dense, white, minute, stellate hairs and longer, patulous or subpatulous, pale ochraceous ones on the main nerves; young vegetative parts minutely tomentose; fruit large; calyx 2- or 3-lobate.
 7. Leaves subobovate-oblong or elliptic-oblong or oblanceolate, acute, 9–25 x 3–9 cm., with 6–8 secondary nerves on each side; petal-lamina and erect staminodes yellow; fruit ellipsoid-oblong, irregularly sulcate tuberculate, 10–18 x 6–9 cm.
10. **T. angustifolium**
 7. Leaves elliptic-oblong or sublanceolate, 10–25 x 3.5–8.5 cm., with 9–12 secondary nerves each side; petal-lamina small, narrow, red; staminodes red-purplish, very broad, reflexed, covering the stamens and petals; fruit ellipsoid-oblong, constricted above the base and at the top below the apex, 10–20 x 6–8 cm.
22. **T. mammosum**
 4. Leaves coriaceous, firmer and more markedly nervose-reticulate than in the species above.
 8. Leaves ovate-oblong or elliptic-oblong, long-caudate, with curved, ascending secondary nerves, softly velvety or apparently glabrous and shining beneath; growth below the jorquette; petal-lamina sessile; staminodes lanceolate or subulate, erect in bud.
 9. Leaves more or less bullate, softly velvety beneath, heterotrichous with a layer of dense, minute, white, stellate hairs and longer, thin-rayed, patulous, stellate hairs on the nerves. Flowers purplish red on trunk; fruit ellipsoid with 5 protuberant ribs, 8–9 x 6–6.3 cm.
4. **T. velutinum**

9. Leaves flat, with practically homotrichous, cinereous or whitish indument beneath, of minute, white, stellate hairs; larger hairs very rare, the major nerves glabrous.
10. Leaves beneath with glabrous major nerves, the quaternary and minor veins stellate-tomentulose, the areoles densely whitish tomentose.
11. Inflorescences small, on leafy branchlets; flowers small, brownish red; stamens 2-antheriferous; fruit ellipsoid-globose, glaucous, 10 x 9 cm. 2. *T. sylvestre*
11. Inflorescences large, on the trunk; flowers purplish red, larger than above; stamens 3-antheriferous fruit globose-ellipsoid, 10 x 8 cm., yellowish 3. *T. speciosum*
10. Leaves beneath with completely glabrous veins, only the smallest veins of the reticulum subglabrous with scattered mediocre hairs, the areoles with very appressed tomentum of minute, white, stellate hairs, the leaf surface with a glabrous appearance.
12. Flowers 12-13 mm. long; petal-lamina suborbicular 5.5-7 x 5-6.5 mm. long; staminodes lanceolate-subulate, 10-12 mm. long; stamens usually 3-antheriferous, also 2-antheriferous; fruit ellipsoid, obtusely pentagonal, 10-11 x 5-5.5 cm. 5. *T. glaucum*
12. Flowers 8-10 mm. long; petal-lamina elliptic, suborbicular or orbicular, 2.5-4 mm. long; staminodes 6-9.5 mm. long; stamens 2-antheriferous; fruit ellipsoid-oblong, more or less pentagonal; 12-25 x 5.2-8 cm. 6. *T. bernouillii*
8. Leaves broad or oblong with regularly spreading, pinnate, secondary nerves, cinereous or ferruginous tomentose beneath, with prominent venation; growth above the jorquette; petal-lamina pedicellate or very reduced; staminodes broadly oblong. Stamens 3-antheriferous.
13. Inflorescences on leafy branches.
14. Leaves beneath monotrichous, glaucous, covered by minute, white, intricate, stellate hairs, the main nerves glabrous with scattered reddish, callous spots; young vegetative parts with ferruginous, floccose-lanate, deciduous indument; calyx trilobate; fruit large, ellipsoid, smooth, 16-25 x 10-12cm.; stipules persistent. Flowers dark red 15. *T. grandiflorum*
14. Leaves beneath heterotrichous, with minute, white, densely intricate, stellate hairs covering the surface, and larger, thicker, reddish or ochraceous stellate hairs on the veins; calyx 5-lobate; fruits ellipsoid, smooth, 7-11.5 x 4-6.6 cm.; stipules caducous.
15. Young branchlets hirsute or hirsute-tomentose; leaves with long, spreading radiate hairs beneath.
16. Pedicels 5-10 mm. long; peduncles 5-10 mm. long; sepals about 10 mm. long; staminodes and petals not ciliate. 20. *T. sinuosum*
16. Pedicels almost lacking (up to 1 mm. long), peduncles up to 6 mm. long; sepals about 7 mm. long; staminodes and petals ciliate 21. *T. canumanense*
15. Young branchlets and leaves beneath subappressed-tomentose.
17. Bracteoles broadly ovate or orbicular. Staminodes obovate-oblong, rounded at apex; petal-lamina oblong, obovate spatulate; ovary densely tomentose 19. *T. nemorale*
17. Bracteoles linear.

18. Staminales scarlet, lanceolate, acute, or subacute; petal-lamina scarlet, orbicular or suborbicular; ovary glabrous or very sparsely granular 17. **T. subincanum**
18. Staminales brownish red, obovate-oblong, rounded or subspatulate at apex; petal-lamina obovate, subrhombic; ovary densely tomentose 18. **T. hylaeum**
13. Inflorescences on trunk and branches. Leaves usually large and thickcoriaceous, strongly nervose beneath; stipules persistent.
19. Flowers yellow.
20. Indument of leaves beneath subvelvety, the minute stellate hairs on veins slightly larger than those of the surface; stipules oblong-lanceolate, subacute; fruits ellipsoid-oblong, obtusely pentagonal narrowed at apex, 25–35 x 10–12 cm. . . 11. **T. cirmolinae**
20. Indument of the leaves beneath, tomentose, the hairs on the veins ferruginous, larger than those of the surface; stipules ovate, obtuse; fruits ovoid-ellipsoid, rounded at both ends, smooth, 18–22 x 9–11 cm. 12. **T. stipulatum**
19. Flowers purple-red.
21. Leaves obovate-oblong with three kinds of hairs beneath (minute, mediocre, and longer); stipules lanceolate; fruit ellipsoid-oblong, rounded at apex, 16–40 x 6–11 cm. . . 14. **T. simiarum**
21. Leaves oblong-elliptic or ovate, usually rugose, with two kinds of hairs beneath (minute and larger); stipules ovate, rather obtuse; fruit ellipsoid-ovoid, rounded at base, obtuse at apex, 19–20 x 10–11.5 cm. 13. **T. chocoense**

Section I. Rhytidocarpus

Theobroma sect. *Rhytidocarpus* Bernoulli, Uebers. Art. *Theobroma* 9. 1869.
Sect. *Eutheobroma* subsect. *Rhytidocarpus* (Bernoulli) Pittier, Rev. Bot. Appl.
10(110):779. 1930.

Petal-lamina very shortly stipitate, subsessile. Petal-hood 1-nerved. Staminales linear-oblong, obtuse, thick, erect in aestivation. Filaments 2-antheriferous. Fruits subglobose-ellipsoid with hard pericarp, strongly costate and reticulate-nerved, minutely tomentose, the mesocarp thick-woody, very hard. Cotyledons epigeous at germination. Leaves beneath, appressed stellate-tomentose. Primary leaves palmatinerved, regular leaves subpalmatinerved, the base 5–7 nerved. Inflorescences axillary or extra-axillary on leafy branches. Sympodial growth of stem by orthotropic, adventitious, lateral-subterminal shoots. Primary branches ternate, deciduous in age, leaving a naked stem; leafy crown lax, flat. Secondary branching dichotomous.

TYPE SPECIES.—*Theobroma bicolor* Humb. & Bonpl.

A single species known.

1. **Theobroma bicolor** Humb. & Bonpl. FIGURES 2, 5, 9, 12, 18, 35; MAP 3
Theobroma bicolor Humb. et Bonpl. Pl. Aequin. 1:104, pl. 30. 1806; H. B. K.
(1823) 317; Triana & Planch. (1862) 208; Bernoulli (1869) 9, pl. 4; Schumann in Mart. (1886) 73; Jumelle (1899) 21, figs. 10, 11; Preuss (1901)

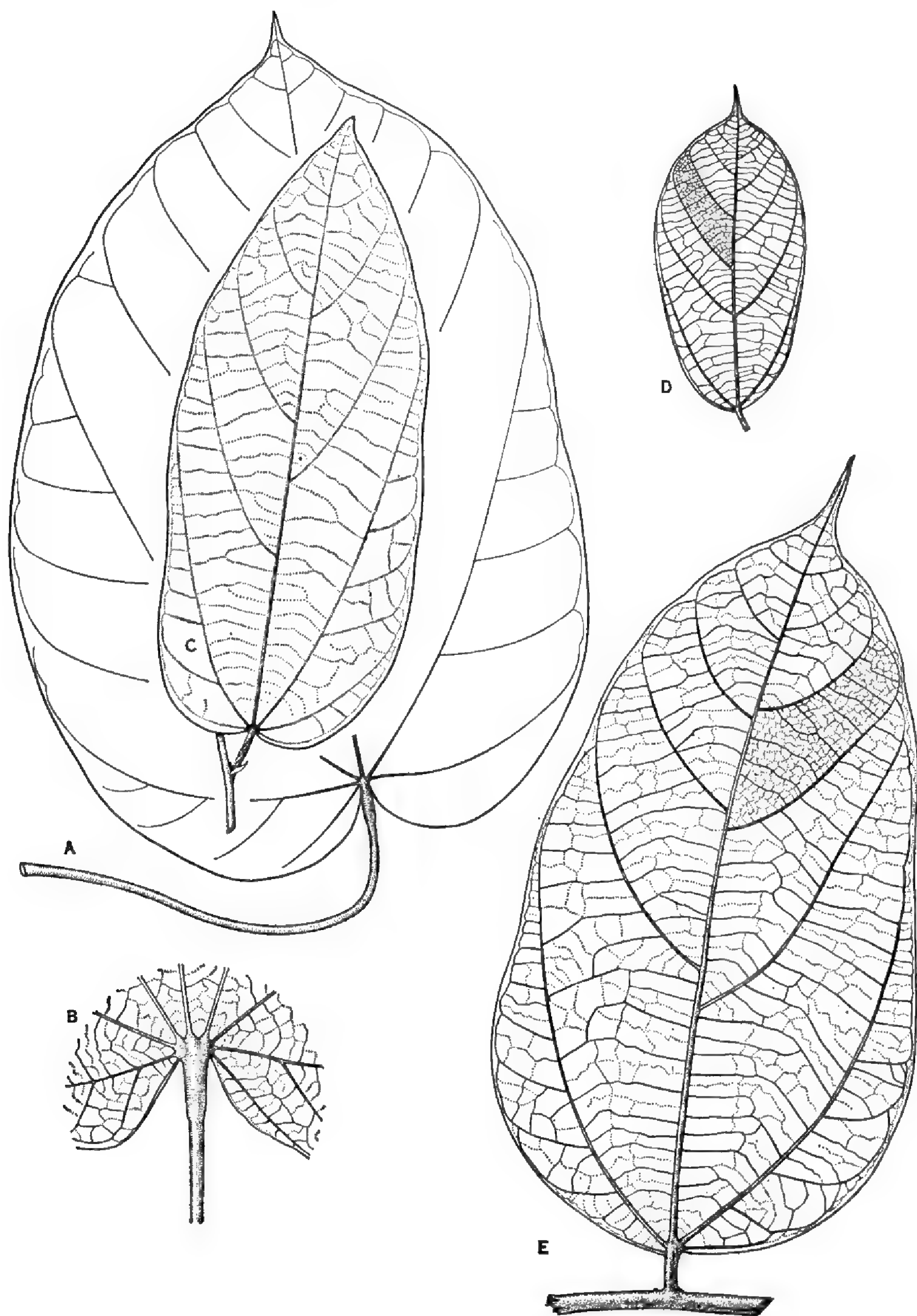


FIGURE 12.—Leaves of *Theobroma*, $\times \frac{1}{3}$: A, *bicolor*, from orthotropic branches (Dawe 83), from above; B, base of same from underside; C, *bicolor* from plagiotropic (current) branches (Kill. & Smith 30006); D, *speciosum* var. *coriaceum* (Huber 1567); E, *velutinum* (Benoist 516).

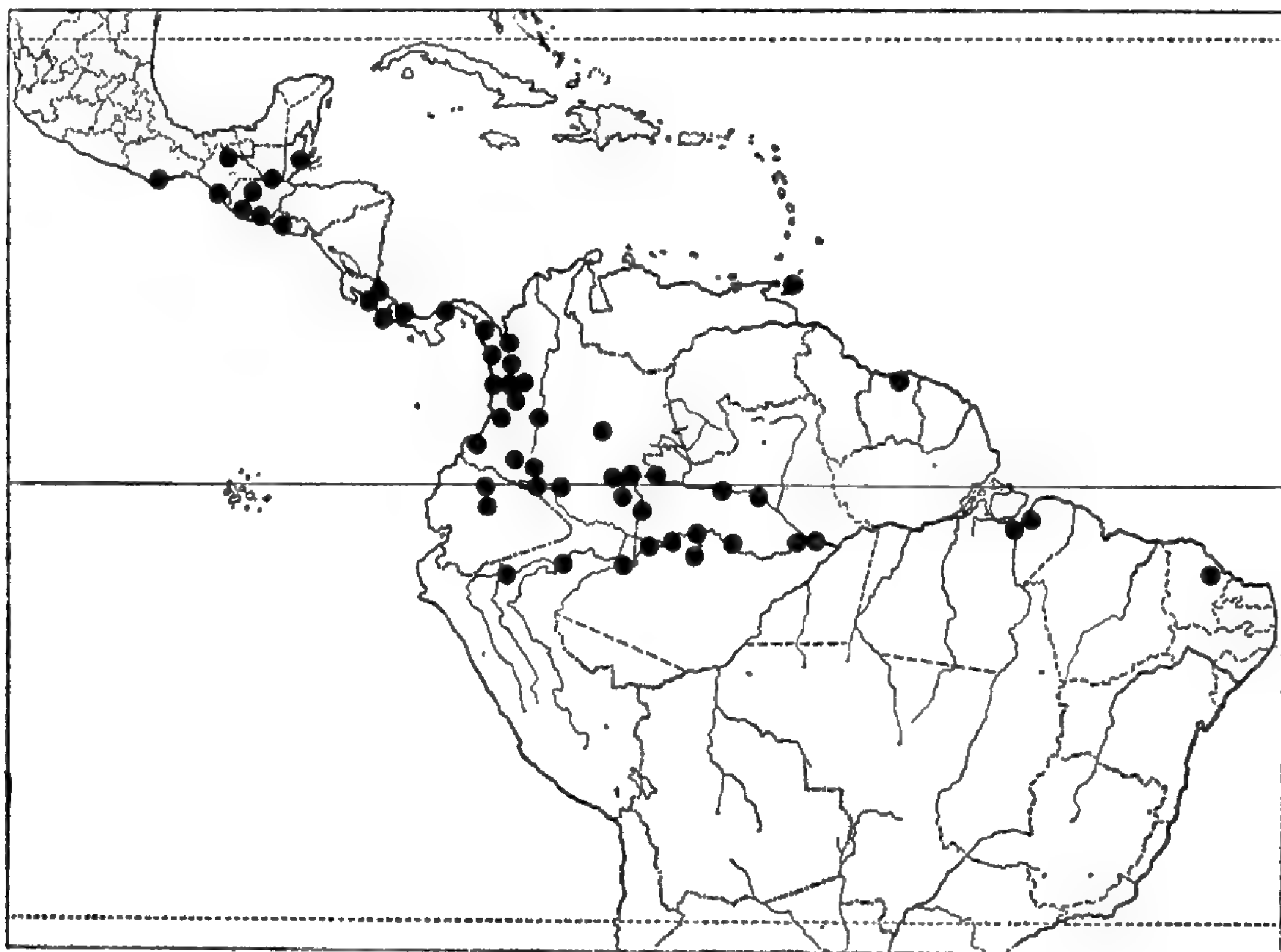
251, 255, *pls.* 3, 4; De Wildeman (1902) 94; Huber (1906a) 274; Standley (1923) 808; Ducke (1925) 132; (1940) 269, *pl.* 1, *fig.* 2; (1954) 13; Standley (1937) 687; Chevalier (1946) 276; Standl. & Stey. (1949) 422; Holdridge (1950a) 3; Addison & Travares (1951) *pls.* 10, 13, *fig.* 8; Baker, Cope & al. (1954) *fig.* 9; Cuatrecasas (1956) 652; León (1960) 313, 315 *fig.*

Theobroma ovatifolia Moc. & Sessé ex DC. Prodr. 1:485. 1824; Icon. Fl. Mex. DC. *pl.* 113.

Cacao bicolor (Humb. & Bonpl.) Poir. in Lam. Encycl. Méth. Suppl. 2:7. 1811.

Tribroma bicolor (Humb. & Bonpl.) Cook, Journ. Washington Acad. Sci. 5:288. 1915; Contr. U.S. Nat. Herb. 17(8), *pls.* 46, 47, 48, 49, 50, 52, 54, 1916.

Theobroma cordata Ruiz & Pavón, Fl. Peruv. Chil. vol. 6, *ined.*



MAP 3.—Geographical distribution of *Theobroma bicolor*, based on specimens mostly from planted trees.

TYPES.—*Humboldt & Bonpland*, Colombia (P). *Mociño & Sessé*, Mexico (of *T. ovatifolia*).

Commonly a small tree 3–8 m. tall, attaining in high forest a height of 25–30 m., with rather narrow crown; sympodial growth by lateral, subterminal, upright shoots; trunk erect with light bark and white wood; primary branches ternate, dichotomous, spreading; young branchlets often horizontal or pendulous, more or less flexuous, subterete, densely and appressed cinereous tomentose with minute

stellate hairs; older branches glabrate, smooth, gray; stipules oblong-lanceolate, 5–8 mm. long, 1.2–2 mm. broad, minutely appressed-tomentose, more or less persistent.

Leaves subpalmatinerved, firmly chartaceous, green above and silvery greenish or silvery cinereous, sometimes pale ochraceous beneath; petiole rather thick, subterete, rigid, minutely appressed-tomentose, 12–25 mm. long, transversely rimose when old; blade oblong-ovate or elliptic-ovate, more or less deeply cordate or emarginate, asymmetrical at base, attenuate, abruptly acuminate at apex, entire or rarely sinuate at the upper margin, 12–34 cm. long, 6–18 cm. broad, the acumen triangular, 6–12 mm. long, glabrous above or with scattered stellate or furcate hairs, green or when dry, pale brownish, the main nerves noticeable, the lesser slightly conspicuous, cinereous beneath, covered with a dense layer of intricate, white, sericeous, stellate hairs, at base 5–7-nerved, the thicker costa and 2 or 3 main nerves on each side strongly prominent, the interior, basal nerves upright, ascending, the 1 or 2 exterior basal pairs arched, spreading, thinner, on the $\frac{3}{4}$ upper part with about 4 secondary nerves each side, prominent, ascending, near the margin curved and vanishing, the tertiary transverse nerves prominent, the lesser prominulous veins minutely reticulate; leaves of young upright (orthotropic) shoots larger, symmetrical, long-petiolate, the blades broadly ovate, deeply cordate, more markedly palmatinerved, 30–50 cm. long, 21–36 cm. broad, the petiole 10–38 cm. long, thickened-pulvinate at both ends.

Inflorescences axillary or extra-axillary on leafy, juvenile branchlets, usually 3–6 cm. broad, with very short axis and divaricate, dichasial and cincinnate branching; branchlets and pedicels angulate, densely ochraceous or cinereous tomentose; peduncles very short, supporting an articulate pedicel subtended by a bracteole; pedicels erect, tomentose, 3–6 mm. long; bracteoles lanceolate, subacute, rather thick, more or less curved, densely and minutely tomentose, 1.5–2.5 mm. long, 0.6–1 mm. broad; buds oblong-ovate, subacute, slightly 5-angulate, densely adpressed and minutely cinereous or ochraceous tomentose.

Sepals lanceolate or ovate-lanceolate, acute, shortly connate at base, spreading and more or less curved-inflexed, 5–6 mm. long, 2–2.5 mm. broad, 3-nerved and sparsely pilose inside, glandular at base, subappressed stellate-tomentose and reddish outside, the margin minutely whitish tomentellous.

Petal-hoods 2–2.5 mm. long, 1–1.2 mm. broad, submembranaceous, whitish rosy, or reddish with darker midrib, oblong-obovate-elliptic, rounded-cucullate, emarginate, auriculate and incurved apex, glabrous with a thick trifurcate midrib inside, hirtellous-pubescent with a depressed tomentellous midrib outside; lamina rather carnose, red,

brownish red or purplish, ovate, rounded at apex, abruptly contracted at base in short nail, articulate to the claw, hirtellous pubescent, 1–1.2 mm. long, 0.8–1 mm. broad, the nail 0.2–0.3 mm. long, erect in bud.

Androecium tube 1.5–1.8 mm. long; staminodes 5 mm. long, brownish red, usually lighter red toward the base with whitish margin, carnose, linear-oblong, obtuse or subacute, slightly narrowed at base, copiously covered with minute, thickish, patulous hairs, erect in bud, 3.5–4.5 mm. long, 0.6–0.8 mm. wide; filaments compressed, curved, reflexed, glabrous, about 1–1.5 mm. long, shortly 2-furcate, 2-antheriferous; anther lobes ellipsoid, 0.2–0.3 mm. long; ovary obovate-oblong, sharply 5-costate, greenish white, velutinous-tomentose, 1.8–2 mm. long, 1–4 mm. broad; styles whitish, about 1.7 mm. long, united, rigid.

Fruits subglobose-ellipsoid, oblong-ellipsoid, or ovoid-ellipsoid, 15–20 (10–25) cm. long, 9–12 (–15) cm. broad, green, when ripe yellow or brownish; pericarp hard, strongly 10-costate, the commissural ribs thick and elevated, the 5 alternate similar but diminishing in thickness towards the apex, the deep furrows reticulate (ligno-nerved), deeply lacunose; pericarp composed of three layers: 1) carnose endocarp about 2 mm. thick, 2) woody, very hard, ribbed and nerved mesocarp, 3–6 mm. thick, 3) firm, carnose becoming coriaceous epicarp 1–2 mm. thick with an outer, densely stellate-pilose epiderm, the whole pericarp about 7 mm. thick on the furrows and 14–15 mm. thick on the ribs; pulp surrounding seeds fibrose, yellowish, sweet, scenty; seeds arranged in 5 rows, complanate, ovoid-amygdaliform, 16–30 mm. long, 14–23 mm. wide, 8–13 mm. thick; embryo white; germination epigeous.

Theobroma bicolor is unique in the genus, easy to recognize by its small, lax crown of few whorls of horizontal, dichotomous branches topping a naked stem, and by its leaves, fruits and flowers. The large papery, firm leaves are whitish silvery beneath and those of the upright shoots are larger, palmatinerved, cordate, and very long petiolate. The flowers are small and pale red generally. The large fruits are strongly ribbed and nerved, with a hard, woody, carved shell; they keep the green color until ripening, when they become yellow or brownish, falling from tree.

COMMON NAMES.—In English: Patashte. Mexico: Patashte, patashtle, pataste, petaste, patatle, petaxte, patasht, pataste de sapo, pataste simarron, cacao malacayo, cacao blanco. Guatemala: Patashte, pataxte, patasht, balamati, balam (*Kekchi*), pec (*Pokonchi*). Costa Rica: Pataste, pataiste, skar-ub (*Bribri*), uerba (*Terraba*), scarbo (*Bribri*), carvu (*Kabekara*), saparón (*Estrella*), erefa (*Guatuso*). Panamá: Pataste, cu-lu-hu (*Choko*). Colombia: Bacao (general), ca-

cao silvestre, cacao marraco, and marraco (in Caquetá). Ecuador: Patas, cacao blanco. Peru: Macambo, majambo, najambu. Brazil: Cacao do Peru (Belém), cupuassú, cupua-í, cacao bafú, cacao bravo.

The Anglo-Colombian Cocoa Expedition (Baker, 1953) recorded the following names: heé-a (*Maku*), (Piraparaná, Taraira); aõ (*Makuna*) (lower Piraparaná, Popeyacá); la-na-pee-tá-ma-ca-la-chu-na-ni (*Yakuna*) (Miritiparaná); há-ha (*Tanimuka*) (Guacayá); maraca bacao (Chocó).

USES.—The pulp is frequently eaten or used by natives to prepare refreshments although its flavor is not very attractive. The seeds are used in many places like those of cacao, giving a chocolate of inferior quality; it is also locally used to manufacture pastry and candy. The seeds of *T. bicolor* have been commercially mixed sometimes with those of cacao. They are poor in theobromine but they have a great proportion of a good quality cocoa butter. In Guatemala the seeds are known in commerce as “tiger” “wariba” or “patashte” cacao (Standley).

According to Llano (1947), in Colombia this species has been tried for grafting but the bark heals with difficulty.

The hard shells of the pod are used locally, as containers like those of *mate* or *tutuma* (*Crescentia cujete*). According to Tafalla it is called “cacao de Castilla” in the Ecuadorian region of Uchiza, where the shells of the pods are smoothed to be used as bowls.

DISTRIBUTION.—*Theobroma bicolor* is widespread in cultivation throughout all humid tropical America, from southern Mexico to Bolivia and Brasil. It is never cultivated extensively, but a few trees can always be seen where cacao is cultivated, and usually also in backyards of tropical farms and in secondary growth. It is frequently found also subsontaneous in more or less open thickets. I have always seen the species in cultivation only. Its true native place is uncertain. Probably it originated in Central America where it is said to be found in primary forests. Miranda (l.c.) writes “se encuentra en acaguales de las selvas altas” in Chiapas; Steyermark found it in dense forests of the region of Ixcán (Huehuetenango) in Guatemala. Another possible original region is the eastern region of Peru and Ecuador. Ynes Mexía recorded it from dense forests in the Napo-Pastaza river basin. Llewellyn Williams found it spontaneous in secondary growths in Loreto. But thus far I have no assurance of a place where it is incontestably native.

MEXICO: Herbarium Sessé et Mociño No. 3620, preserved at the Madrid Botanical Garden “Plantae Novae Hispaniae a Sessé, Mociño, Castillo et Maldonado lectae (1787–1795–1804)-*Theobroma Patastle* Ic. N.” (MA, lectotype of *T. ovatifolium*; BM, F, G, isotypes); the MA specimen has foliage, inflorescences and flowers and may be considered the holotype of *Theobroma ovatifolium* Mociño

et Sessé ex DC.; I select it as the lectotype; it is photograph FM No. 48412. The Chicago specimen is a duplicate of this and has only one leaf; the very good British Museum specimen, and two at Geneva are certainly isotypes in spite of not bearing the name of Sessé and Mociño and having "*Theobroma Patastle*, N.E." as only information; some specimens have the indication "Herb. Pavón," having been sent by Pavón from Madrid. The collections with the number 3621 Sessé et Mociño et al. (MA) are paratypes and may be duplicates of 3690, having been numbered recently (in 1935); they include normal foliage and inflorescences and juvenile long-petiolate, broadly cordate leaves (FM photographs 48414 and 48413). The photograph FM 30526 is from plate 485 of the Mociño and Sessé Flora Mexicana, No. 113 in De Candolle's copies.

OAXACA: Pochutla, Capital Rancho Viejo; tree 15 m., flowers purple, "cacao malacayo," Feb. 1941, *Reko* 6068 (F).

CHIAPAS: Acagoyagua, Escuintla, "pataste de sapo," 22 VII 1947, *Matuda* 16733 (F). Ibidem, "pataste simarrón," fruit only, 6-7 x 4 cm., 28 VIII 1947, *Matuda* 16840 (F, MEXU). Esperanza, Escuintla, "pataste," cultivated, 11 VIII 1947, *Matuda* 16690 (BR, F, MICH, MEXU, NY). Palenque, 100-150 m. alt.; tree up to 25 ft. tall; commonly cultivated around Palenque for its fruits; fruits yellow; seed ground and mixed with cornmeal for making "pazoli"; flowering and fruiting in May; said to be common in the forests on the slopes above Chacamax River, V 1937, *Ll. Williams* 9345 (F, Y).

GUATEMALA: Without locality, "cacao," 10 V 1914, *Davidson* s.n. (US). ALTA VERAPAZ: Trece Aguas, cacao plantation at Cacao, "petaste" or "patashte," 9 III 1914, *Cook & Doyle* 50 (US); Trece Aguas, near Finca Sepacuité, "petaxte" IV 1905 (leaf from upright stem of young tree), *Cook* 4 (US). Ibidem, Chirujija Oxee, near Finca Sepacuité, "balamati," 25 V 1902, *Cook & Griggs* 756 (US). Chama, 900 ft. alt.; tree 25 ft., flowers reddish, fruit large, hard shelled, "patashte" cultivated by Indians; used similarly to cacao, rather sweeter in flavor, 15 VI 1920, *H. Johnson* 237 (F, US). Cubilquitz, 350 m. alt., VI 1901, *von Tuerckheim* 7824 (GH, K, NY, US). Vicinity of Sibiete, 370 m. alt., small tree 25 ft. tall, leaves firmly membranaceous, deep green above, gray silvery beneath; flowers with grapy-purple calyx, "balam" (*Kekchi*), "patasht" (Spanish), cultivated, 12 III 1942, *Steyermark* 44941 (F).

HUEHUETENANGO: Sierra de los Cuchumatanes, 150-200 m., between Ixcán and Río Ixcán; tree 30 feet tall, leaves membranaceous, papyraceous, dark green above, silvery green beneath; dense rich forest, 23 VII 1942, *Steyermark* 49317 (F, US). Huehuetenango, 1800 m. alt., seeds in market brought here from the Pacific Coast, *Standley* 82446 (F).

SANTA ROSA: Region of Platanares, between Taxisco and Guazacapán, 220 m. alt.; wet forested quebrada, simple shrub 3-4 m. tall; escaped here, 3 XII 1940, *Standley* 79069 (F).

SUCHITEPEQUEZ: Mazatenango, cultivated, III 1865, *Bernoulli* 94 (F, G, NY). Ibidem, III 1865, *Bernoulli & Cario* 3145 (GOET).

BRITISH HONDURAS: Conservation Forests H. 2192/29 (F, GH, UC). Stann Creek Valley, Big Eddy Valley; tree 13 inch diameter, fruit 8 inch long, "pataste," "mountain cacao," 16 XII 1840, *Gentle* 3464 (F, GH, MICH, MO, NY, U).

EL SALVADOR: Sonsonate, cultivated, "patashte," "pataste," 20 IV 22, *Calderón* 23610 (F, GH, MO, NY, US); ibidem, "pataste," 1922, *Calderón* 627 (GH, NY, US).

COSTA RICA: Peninsula Osa ad Golfo Dulce, circa Puerto Giménez, ad litus; arbor 6-8 m., floribus purpureis, 15 IV 1930, *Cudofontis* 92 (WU). Vicinity of Guapilés (prov. Limón), 300-550 m. alt.; planted tree 25 ft., flowers dull red 12,

13 III 1924, *Standley* 37374 (US). Puerto Giménez de Osa and vicinity, 14 IV 1930, *Brenes* 12333 (Herb. Nac. C.R. 212) (F, NY). Edge of the road to Tuis, 650 m.; tree with spreading branches, "pataste" or "pataiste," XI 1897, *Tonduz* 11304 (F). Tucurrique, grassland at Las Vueltas; tree 40 cm. diam., 15–20 m. high, 635 m. alt., "pataste," "pataiste," III 1899 *Tonduz* 13110 (G, P, US). Hacienda Baltimore (Limón), 10 m. alt., in a small plantation of this species, 8 VII 1949, *Holdridge* s.n. (TURRI). La Lola, planted, 6 XI 1961, *Cuatrecasas & Paredes* 26534 (US).

PANAMA: Bocas del Toro, in Laguna de Chiriquí and its neighborhood, Pope's Island, XI, XII 1885, *Hart* 158 (US). Darién, Headwaters of Río Chica, 500–750 ft.; tree 35 ft.; flowers dark red; cultivated by Choco Indians, "cu-lu-hu," *Allen* 4593 (G, MO, NY). Canal Zone, along Caño Quebrado, 2 XII 1914, *Pittier* 6883 (GH, NY, US).

TRINIDAD: L'Eranché Est, Sangre Grande, 10 VII 1929, *Boehlmer* 12229 (TRIN). Blue Basin, 2½–3 miles distant, 21 IX 1928, *Lange* 12056 (TRIN). Grounds of I.C.T.A., River Estate Diego Martínez, field 19; fruits 19.3 x 13.3 cm., yellowish at maturity, specimen from seeds brought from Jinogojé, Apaporis, Colombia, 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25784T (US); same field; calyx pale red, hoods with darker midrib, petal-lamina very small, brownish red, staminodes brownish red, lighter reddish toward the base, with whitish margin, styles whitish, ovary greenish white, 1 IX 1961, *Cuatrecasas & Cope* 25795 (US). Tree from seeds from La Pedrera, Colombia; fruits 16.2 x 14 cm., 31 VIII 61, *Cuatrecasas, Cope, & Bartley* 25787T (US). Field 2; fruits 15 x 10, 16 x 10.8, 16.5 x 10, 18.2 x 11.2, peduncle 0.7–0.9 cm., 31 VIII 61, *Cuatrecasas, Cope, & Bartley* 25786T (US).

SURINAM: Paramaribo Gardens, cultivated, VI 1910, *Stockdale* s.n. (K, U).

COLOMBIA: ANTIOQUIA: Savaletas, 100–500 m., XII, *Lehmann* 7909 (K).

TOLIMA: Ibagué, II 1916, "cacao silvestre," *Dawe* 83 (US).

HUILA: Valle del Magdalena, Garzón, IV 1845, *Goudot* s.n. (G, P).

EL VALLE: Palmira, Granja Agrícola, 900 m. alt. "bacao," *Duque Jaramillo* 1205 (F). Ibidem, X 1943, *Llano* s.n. (COL, F). Palmira, 925 m., cultivated in grounds of experiment station (said to have been brought from the Chocó); tall, erect tree, leaves hanging vertically, almost white beneath, flowers dark red with maroon staminodes, fruit oblong, green with the furrows strongly rugose, 29 X 1944, *Fosberg* 21310 (NY, UC, US). Palmira; tree 4 m., "bacao," I 1947, *Duque Jaramillo* 4403A (COL). Ibidem; tree 3 m., flowers red, "bacao," 3 XII 1947, *Cardenosa, Murgueitio, & Barkley* 17C934 (COL, F). Cartago, *Goudot* s.n. (P, WU). Pacific Coast, Río Calima, La Trojita, left side of river, 5–20 m. alt.; tree 3 m., "bacao," 27 II 1944, *Cuatrecasas* 16526A (F, VALLE) (fruit only). Buenaventura (and Tumaco) 0–400 m., fl. perpetual, *Lehmann* 9021 (K, NY).

CHOCÓ: "Nvelle. Grenade, Chocó," "bacao," *Humboldt and Bonpland*, s.n. (P, holotype). *Bonpland*, probably isotype, from Paris (F). Near Istmina, road to Cértegui, in forest, 75 m. alt.; tree 6 m., flowers red, "bacao," 3 VII 1944, *García Barriga* 11178 (COL, US). Chocó (i Barbacoas), 25 m. alt., "bacao," IV 1853, *Triana* 5333 (–3) (BM, COL). Ciudad Mutis, 27 X 1946, *Romero Castañeda* s.n. (COL).

NARIÑO: Pacific Coast, Amarales, "bacao," 1866, *Triana* s.n. (BM, BR, COL, G, K, NY, WU).

CAQUETÁ: Solano, 3 km. SE of Tres Esquinas, on Río Caquetá, below mouth of Río Ortegúaza, wet tropical forest of Amazon basin; tree 8 m. high, 10 cm. DBH; dark brown, smooth, lichen patches, flowers red; watermelonlike fruit 18 cm. long, 10–11 cm. broad, yellow, edible; Indians plant it; secondary lowland forest, river bank; possibly an escape from cultivation; several cultivated trees

seen March 13 walk near Río Caquetá, 2 km. s. of Solano; "cacao marraco," 6 III 1945, *Little & Little* 9598 (NY, US).

PUTUMAYO: Vicinity of Mocoa; small tree 4 m., sterile; apparently cultivated, 17 III 1953, *Holliday & Cope* T 77 (COL, TRIN, US).

VAUPÉS: Río Negro, near San Felipe, Caño Mayabo, river level; tree 4-5 years old, introduced on a house site, 27 X 1952, *Baker* 34 (COL, F, TRIN). Río Inírida, right bank below mouth of Caño Caribe; tree 25 m. high, 1 m. diameter at ground level, growing on slope just above high watermark; overtopping the surrounding forest; not thought to be wild. 23 I 1953, *Bartley & Holliday* T66 (COL, TRIN, US). Río Vaupés, opposite confluence with Río Papurí, Yavaraté, Silesian Mission São Miguel; trees 3-4 years old from seed brought by Indian from the interior of Colombia, 20 II 1952, *Bartley & Holliday* T 47 (COL, TRIN, U, US). Caño Umuña, Río Piraparaná, river level; cultivated tree in Indian garden, 8 IV 1952, *Baker & Cope* 11a (TRIN). Jinogojé, on Río Apaporis, small tree 15 ft. cultivated in Indian garden, 23 VIII 1952, *Baker & Cope* 2 (TRIN). Río Apaporis, Gino-Gojé, between the rivers Piraparaná and Popeyacá, 250 m. alt.; tree 4 m., leaves white below, 3-11 IX 1952 *García Barriga* 14416 (US).

AMAZONAS: Río Caquetá, La Pedrera, river level; tree 30 ft., presumed cultivated, 1 X 1952, *Baker & Cope* 26 (COL, F, TRIN, US). Río Igaraparaná, vicinity of La Chorrera, 180 m. alt.; small tree, cultivated, "marraca," 4-10 VI 1942, *Schultes* 3922 (COL, F).

ECUADOR: *Muller* s.n. (K). Balao; arbor 40 m., in forest, flowers purplish, "cacao blanco," I 1892, *Eggers* 14244 (A, L, LE, M, US). Río Sucumbíos, between Putumayo and Quebrada Teteyé, 260 m., "cacao" (*Kofán*), 29 III 1942, *Schultes* 3471 (NY).

NAPO-PASTAZA: Between Tena and Napo; tree about 15 m. high, petals dark red, staminodia blackish brown, 5 I 1940, *Asplund* 10271 (S). NE of the province, Tiputini-Lagartococha, 20 I-5 II 1953, *Fagerlind & Wibom* 2371 (S). Cantón Napo, near Tena, 400 m. alt., dense forest; tree up to 18 m. high, fruit called "Patás," size of small watermelon, the pulp being eaten and the seeds cooked or raw much appreciated, 2 II-VI 1935, *Mexía* 7214 (F, P, UC, US).

BRAZIL: "Brazil, Dr. Martius," no data (G). Manaquiri forest; 15-30 ft., leaves white beneath, flowers dark purple, *Spruce* s.n. (K).

AMAZONAS: Rio Negro, Barcellos, matta, cult.?, 27 VI 1905, *Ducke* 7202 (BM, MG, US). Ibidem, *Ducke* 7202-B (BM, MG). "Prov. Rio Negro, in sylvis, Martius Obs. 28823, Iter-Brasiliensium 319, *Martius* [862, 863, 864, 865] (M). Rio Negro, Lagos, "cacao bravo," 5 VIII 1874, *Traill* s.n. (GH). Rio Negro, *Schomburgk* 870 p.p. (BM, G, GH, GL, K, OXF, P, US). São Antonio de Iça, capueira, "cupuassú," 3 VIII 1906, *Ducke* 7638 (MG). Município São Paulo de Olivença, basin of creek Belem; tree 40 ft. high, trunk 5 inch diam., planted by Indians 26 X-XII 1936, *Krukoff* 9019 (A, BM, F, G, K, LE, MICH, MO, NY, P, US). Manaus, Campos Salles, 15 m., 20 VIII 1928, *Luetzelburg* 23895 (M). Manaus, Agricultural Experiment Station, 25 m. alt.; tree 30-35 ft., fruit oblong on ultimate branches (25 x 10 cm.), cult.?, 13 X 1929, *Killip & Smith* 30006 (GH, NY, US), fruit collection 681 (US). Experimental Garden of Nord Brazil, cultivated and wild in forest, "cacao d'Anta," 20 VIII 1928, *Luetzelburg* 23065 (M). Ega, "colitur circum Indorum villas, Oct. 1830," *Poeppig* 2746 p.p. (WU); "In Bras. tropica fl. Amazonas Oct. 1839," *Poeppig* 2746 pp. (GOET). Ega, *Poeppig* 2746 p.p. (F, LE). Teffé, forest, 29 VI 1906, *Ducke* 7397 (BM, G, MG, US). Fonte Boa, firm land, medium-sized tree, "cacau bafú," 28 III 1945, *Fróes* 20625 (F, IAN, K, NY, US). Rio Juruá, Santa Clara, cultivated, "cupuaçú" Baum, X 1900, *Ule* 5030 (BM, G, HBG). Rio Juruá, Gaviao; flowers purple, "cupua-i," III 1875, *Traill* 60 (K, P). Rio Sapo, 21 II 1874, *Traill* 60 (K). "Ad oram meridionalem

flum. Amazonum ad ostium flum. Solimoes," VI 1851, *Spruce* 1609 (BM, K, M, P, WU).

CEARA: Ceará, VIII–XI 1838, *Gardner* 870 (G).

PARÁ: Belém, Horto do Museu Goeldi, arvore 483; medium size tree, granate flowers, 10 X 1957, *Cavalcante* 310 (MG, US). Belém, cult., *Pires & Black* 746 (IAN). Belém, I.A.N. cult., "cacau do Perú, 6 XI 1952, *Pires* 4340 (IAN, NY).

PERU: "Theobroma cordata del Perú, sp. nov.," *Ruiz & Pavón* (BM). "Peruvia, Herb-Pavón" (G). Perou, *Pavón* 617 (G). 1909–1914 *Weberbauer* 6245.

LORETO: Mishuyacu, near Iquitos, 100 m.; forest, tree 6 m. high, flowers dark violet and rose, clearing, "macambo," V–VI 1930, *Klug* 1523 (F, NY). Florida, Río Putumayo at mouth of Río Zubineta, 200 m.; forest clearing, tree 4 m., flowers garnet, "macambo," III–IV 1931, *Klug* 2021 (A, F, GH, K, MICH, MO, NY, S, US). Paraíso, upper river Itaya, 145 m.; "najambu," 1 X 1929, *Ll. Williams* 3346 (F, US). Amazon River, Caballo-Cocha, 6 VIII 1929, *Ll. Williams* 2149 (F, GH, US). Maynas, *Poeppig* (L), *Poeppig* 18 (BM). Marañón River from Iquitos to the mouth of Río Santiago at Pongo de Manseriche, ca. 77°30' W., 1924, *Tessmann* 4079 (NY, S).

Section 2. Oreanthes

Theobroma sect. *Oreanthes* Bernoulli, Uebers. Art. *Theobroma* 7, 1869.

FIGURE 4; MAP 1

Sect. *Bubroma* subsect. *Oreanthes* (Bernoulli) Pittier, Rev. Bot. Appl. 10(110):779. 1930.

Petal-lamina sessile, large. Petal-hood 3-nerved. Staminodes linear-subulate or lanceolate, erect in estivation. Filaments 3- or 2-antheriferous. Fruit more or less angulate or costate with coriaceous, tomentose pericarp, the endocarp rigid, thin-lignose. Cotyledons epigeous at germination. Leaves densely, minutely, stellate-tomentose beneath inside the reticulum. Inflorescences many-flowered, on the trunk or, in few cases, small and on leafy branches. Sympodial growth of stem by orthotropic, adventitious, lateral-subterminal shoots. Primary branches ternate, deciduous when old, leaving an unusually long, naked stem. Leafy crown loose, flat. Secondary branching dichotomous.

TYPE SPECIES: *Theobroma speciosum* Willd. ex Spreng.

2. *Theobroma sylvestre* Mart. FIGURES 4, 9, 13, 16, 18; MAP 4; PLATE 1

Theobroma sylvestre Mart. in Buchner, Repert. 35:24. 1830; *Linnaea*, Litt.

Ber. 32. 1831; Bernoulli (1869) 14, pl. 7, fig. 1; Schumann in Mart. (1886)

78 (as *T. sylvestre*); Jumelle (1899) 34; De Wildeman (1902) 98.

Theobroma Spruceana Bernoulli, Uebers. Art. *Theobroma* 9, pl. 3, fig. 1. 1869;

Ducke (1925) 131; (1940) 270, pl. 3; (1954) 13; Chevalier (1946) 276;

Addison & Tavares (1951), pl. 5, fig. 1, pl. 6, fig. A, pl. 12, fig. 4; León (1960)

318, 319, fig.

Theobroma nitida Bernoulli, Uebers. Art. *Theobroma* 15, pl. 7, fig. 2. 1869.

Theobroma Martii Schum. in Mart. Fl. Bras. 12(3):78. 1886; Jumelle

(1899) 35; De Wildeman (1902) 98.

Theobroma speciosum var. *Spruceana* (Bernoulli) Schum. in Mart. Fl. Bras.

12(3):75. 1886; Jumelle (1899) 32, fig. 16; De Wildeman (1902) 95.

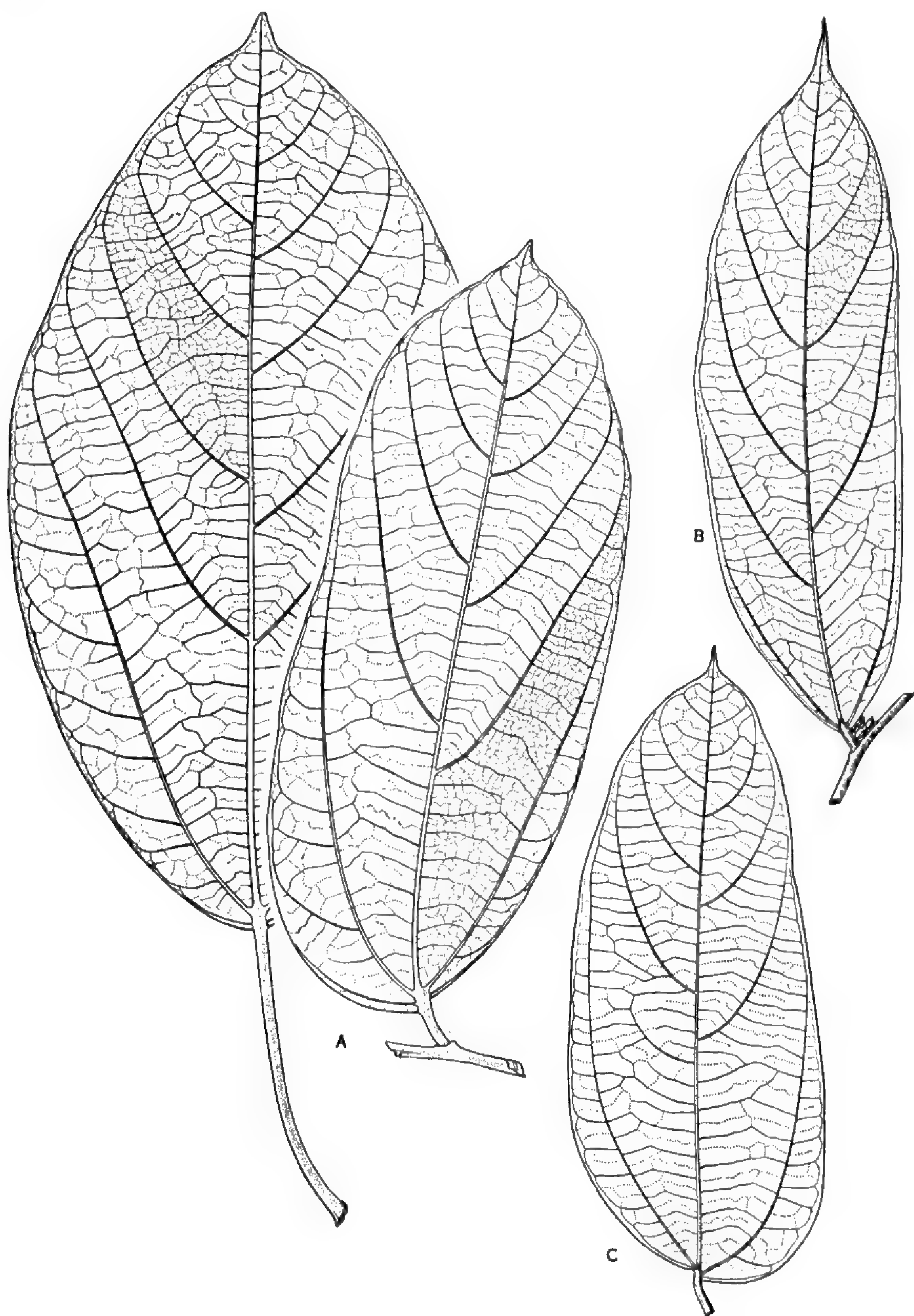
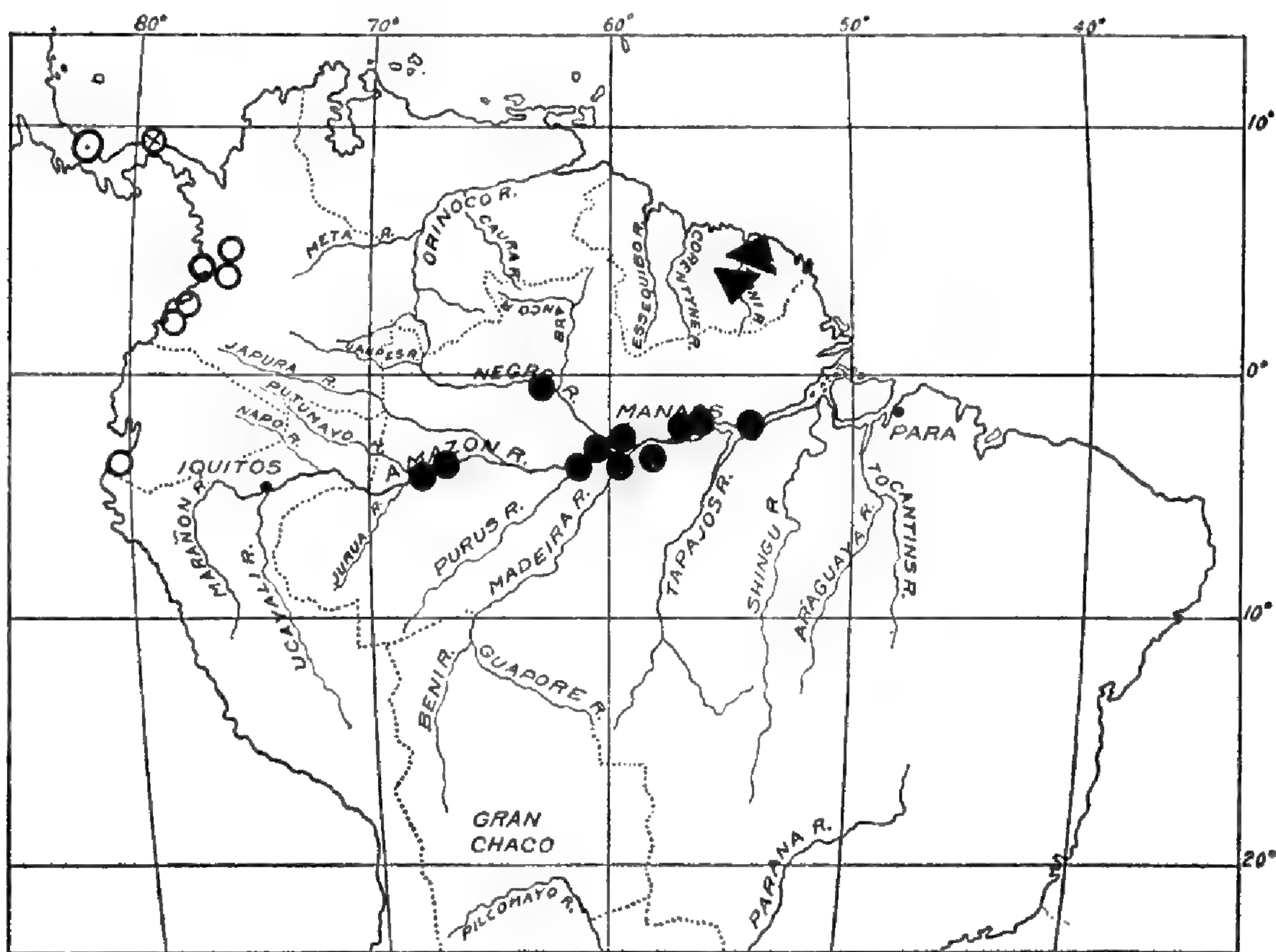


FIGURE 13.—Leaves of *Theobroma*, $\times \frac{1}{8}$: A, *speciosum*, from orthotropic and plagiotropic branches (US-1031918); B, *sylvestre* (US-1693105); C, *sylvestre* (Martius, type).

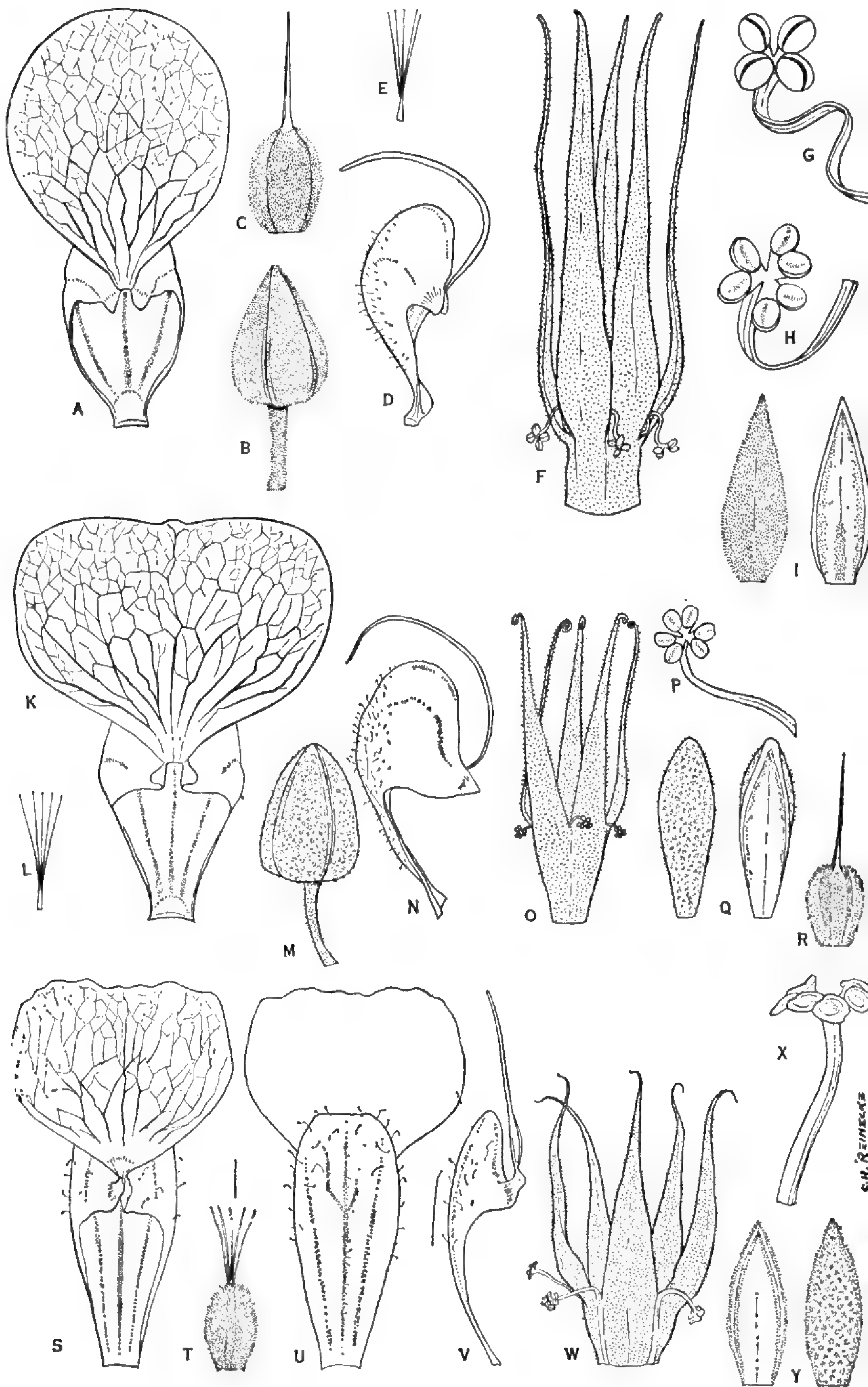


MAP 4.—Distribution of *Theobroma sylvestre*, ●; *T. bernouillii* subsp. *bernouillii* ⊕; *T. bernouillii* subsp. *asclepiadiflorum* ⊙; *T. bernouillii* subsp. *capilliferum* ○; *T. velutinum* ▲.

TYPES.—*Martius*, Brazil, Iter Brasil. 322 (in M, no. 891) (Photo F. M. 19644). *Spruce* 166, Brazil, Pará, Obidos (of *T. Spruceana*). *Martius*, Brazil, Iter Brasil. 322 (in M, no. 890) (Photo F. M. 40709) (of *T. nitida*).

Small- or medium-sized tree up to 12 m. high, sympodial growth by lateral, subterminal upright shoots; primary branching ternate; terminal, leafy and floriferous branches dichotomous, terete, rugulose, dark brownish, the hornotinous ones pulverulent, stellate-tomentellous, soon glabrate or glabrous; stipules small, soon deciduous.

Leaves distichous, firmly coriaceous; petiole short, robust, appressed stellate-tomentose, 5–10 mm. long; blades elliptic-oblong with obtusely cuneate, asymmetrical base, often ovate-oblong or oblong-ovate with rounded, asymmetrical base, attenuate and acutely acuminate at apex, the margin entire or slightly sinuose, 12–30 cm. long, 5–8 (–13) cm. broad, the acumen 1.5–2.5 cm. long, rather lustrous above, pale brownish when dry, glabrous, the costa and secondary nerves subfiliform, prominulous, the other nerves almost unnoticeable, paler beneath with tawny nervation, the costa very prominent, the secondary nerves about 6 pairs, prominent, ascending, decurrent, arching and uniting near the margin, the inferior pair forming a much more acute angle, the transverse tertiary nerves distant 5–10 mm. from



[FIGURE 14]

each other, thin and prominent, the lesser veins forming a minute, prominulous reticulum; midrib, secondary and tertiary nerves glabrous, those of the fourth rank subglabrous, the lesser reticulate veins and the areoles covered by dense, minute, whitish, sericeous tomentum of stellate hairs.

Inflorescences small, axillary or extra-axillary on small branches; panicles short, 1–2 cm. long, branched from base, the branchlets 1–8, fasciculate, crowded, scarcely ramulose, densely stellate-tomentose, bracteolate at joints, bracteoles ovate, or ovate-lanceolate, 1–2 mm. long, stellate-tomentose; pedicels 2–5 mm. long, moderately thin, densely tomentose; sepals shortly united at base, thick, sublanceolate-oblong, subacute, involute at margin, ferruginous, stellate-tomentose outside, glabrous inside except for the minutely stellate-tomentose margin and glandular trichomes at base, curvate and spreading at anthesis, 7–9 mm. long, 2–2.5 mm. broad.

Petal-hood thick-membranaceous, trinerved, pale and reddish striate, rugulose, papillose, sparsely pilose outside, oblong-obovate, cucullate-rounded at apex, 4 mm. long, 2 mm. broad; petal-lamina brownish red or rose, rotundate-subreniform, minutely crenulate, rugose, 2 mm. long, 2.2–2.5 mm. broad, suddenly constricted into a short claw, articulate at base; androecium tube 1.5–2 mm. high; staminodes brownish red or rose, linear-subulate, abruptly narrowed-acuminate at apex, the acumen often curled, densely and minutely pilose-muricate throughout, 5–6 mm. long, 0.7–0.8 mm. wide; filaments 1–1.2 mm. long, glabrous, arched, diantheriferous, the lobes of the anthers ellipsoid, 0.4 mm. long; ovary ovoid-ellipsoid, 5-ridged, ferruginous-tomentose, 1.5–2 mm. long, the apex whitish tomentulose; styles 5, thin, acute, connivent, united only at base.

Fruits elliptic-globose, or subglobose, about 6 x 5.8 cm., rounded at apex, umbilicate at base, the pericarp coriaceous, minutely and densely tomentose, glaucous when ripe, about 5 mm. thick, the inner and outer layer hard, thin, the middle one carnose; seeds ovoid-oblong, 1.4–2.1 cm. long and 0.5 x 0.9 mm. broad; pulp rather sweet, scentless, white; fruiting peduncle about 1.8 cm. long, 7 mm. thick.

At the Botanische Staatssammlung in Munich there are several specimens from Martius' trip to Brazil which bear the annotation

FIGURE 14.—A–I, *Theobroma glaucum* (Baker & Cope 11 and 18): A, petal from inside $\times 5$; B, bud, $\times 2$; C, pistil, $\times 5$; D, petal laterally, $\times 5$; E, styles, $\times 5$; F, androecium, $\times 5$; G, 2-antheriferous stamen, $\times 10$; H, 3-antheriferous stamen, $\times 10$; I, sepal from outside and inside, $\times 2$. K–R, *T. speciosum* (Archer 7619): K, petal from inside, $\times 5$; L, styles, $\times 5$; M, bud, $\times 2$; N, petal laterally, $\times 5$; O, androecium, $\times 5$; P, stamen, $\times 10$; Q, sepal from outside and inside, $\times 2$; R, pistil, $\times 5$. S–Y, *T. velutinum* (B. W. 1161): S, petal from inside, $\times 5$; T, pistil, $\times 5$; U, petal from outside, $\times 5$; V, petal, laterally, $\times 5$; W, androecium, $\times 5$; X, stamen, $\times 15$; Y, sepal from inside and outside, $\times 2$.

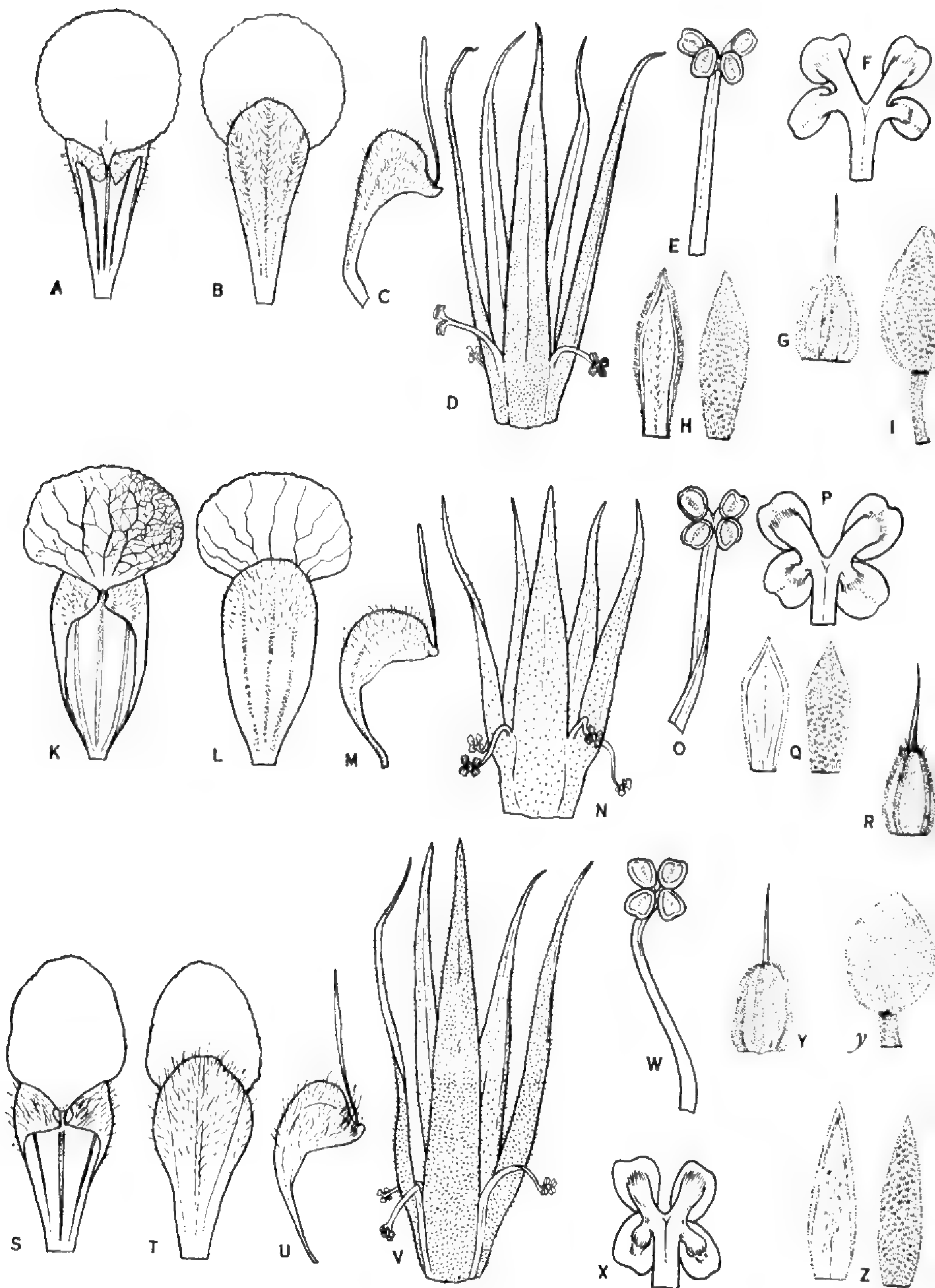


FIGURE 15.—A-I, *Theobroma bernouillii* subsp. *capilliferum* (Holliday 142): A, B, C, petal from inside, outside, and laterally, $\times 5$; D, androecium, $\times 5$; E, stamen, $\times 10$; F, anthers $\times 20$; G, pistil, $\times 5$; H, sepal from inside and outside, $\times 2$; I, bud, $\times 2$. K-R, *T. bernouillii* subsp. *bernouillii* (Pittier 4105): K, L, M, petal from inside, outside and laterally, $\times 5$; N, androecium, $\times 5$; O, stamen, $\times 10$; P, anther, $\times 20$; Q, sepal from inside and outside, $\times 2$; R, pistil, $\times 5$. S-Z, *T. bernouillii* subsp. *asclepiadiflorum* (Wedel 1535): S, T, U, petal from inside, outside and laterally, $\times 5$; V, androecium $\times 5$; W, stamen, $\times 10$; X, anthers, $\times 20$; Y, pistil, $\times 5$; YY, bud, $\times 2$; Z, sepal from inside and outside, $\times 2$.

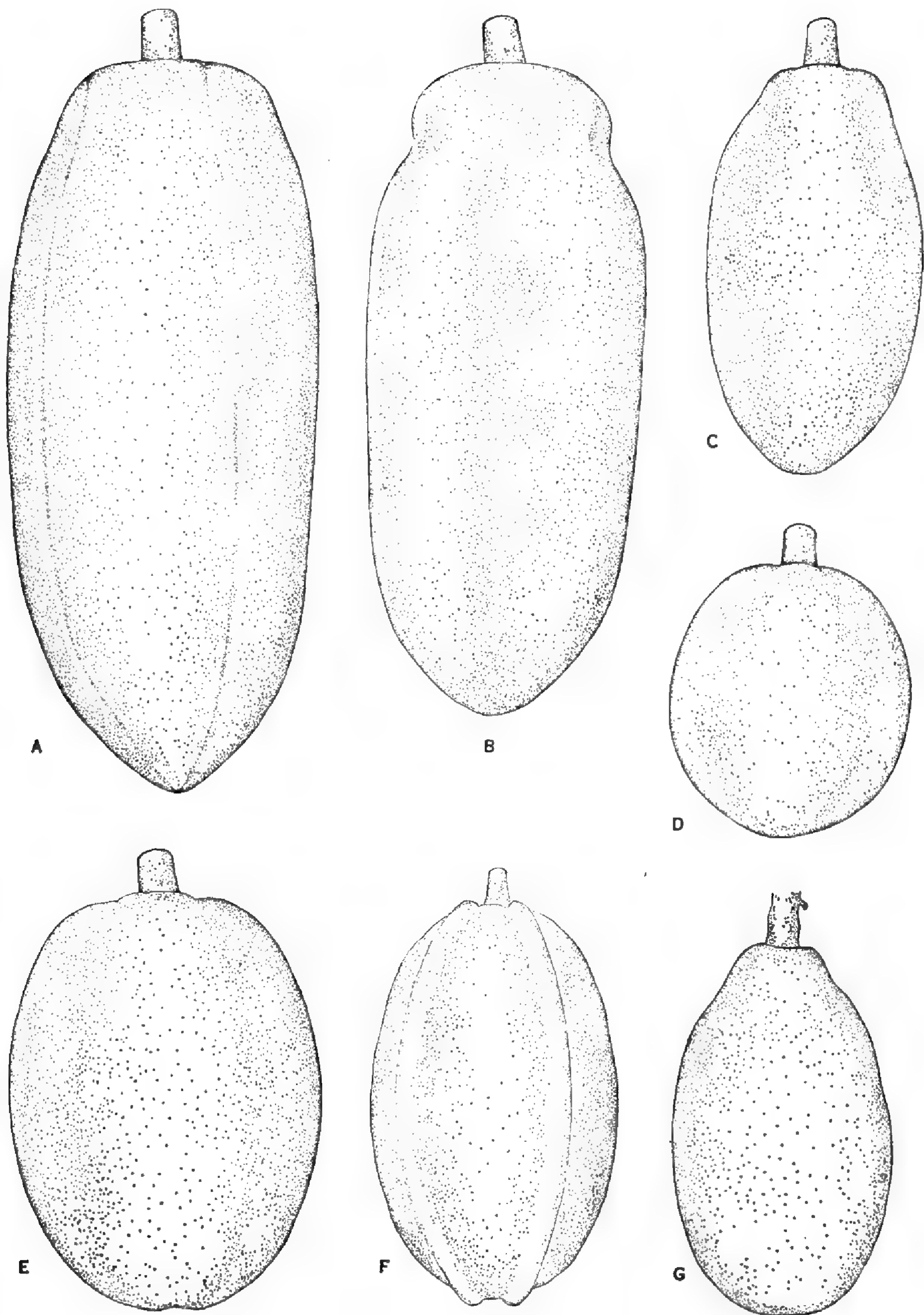


FIGURE 16.—Fruits of *Theobroma*, $\times \frac{1}{2}$: A, *bernouillii* subsp. *asclepiadiflorum* (Lucas 1); B, *bernouillii* subsp. *capilliferum* (Cuatr. 17034); C, *glaucum* (Froes 20645); D, *sylvestre* (Froes 20463); E, *speciosum*; F, *velutinum* (Benoist 516); G, *nemorale* (Cuatr. 21291).

"*Iter brasiliensis*" and then the number 322 at the foot of the label; they are named by Martius as "*T. sylvestris* Martius." All the specimens agree with each other essentially, although some of them have oblong leaf blades, slightly asymmetrical or symmetrical at the base, and others have broad, oblong-ovate blades, very rounded and asymmetrical at the base; in all of them there is a longer distance between the basal pair of secondary nerves and the next pair than between the other pairs of secondary nerves; two of these specimens bear typical rounded, smooth fruits. One of the specimens which shows the number 891 on a mounting strip (Photo F. M. 19644) may be considered as the holotype of *T. sylvestre* (lectotype); it has a leafy branch with the basal half of a fruit, and a loose, broad, obovate-oblong leaf. Bernoulli, without obvious reasons, considered one of the specimens [890] (Photo F. M. 40709) a different species and described it as *T. nitida* Bernoulli. Another of these specimens [871] was named by Schumann as *T. grandiflorum*, and it is mixed with an authentic *T. grandiflorum* specimen on the F. M. 19641 Photograph. After a close examination of the series of Martius types, it was clear to me that there do not exist basic differences between them and *T. spruceanum* Bernoulli. Most of Martius specimens have somewhat thinner and smaller leaves than the current collections, variations which can be attributed to the habitat and to the age of the collected branches.

Schumann listed *T. sylvestre* Mart. under his "Species dubiae."

The binomial *Theobroma Martii* was published by Schumann as a new name for *T. nitida* Bernoulli, although due to some typographical error this name was not quoted as synonym. But Schumann cited "l.c. 15" and quoted unchanged the diagnosis given by Bernoulli for *T. nitida* on page 15. Schumann considered the name a homonym of his *T. nitidum* (Poepp. & Endl.) K. Schum. (*Abroma nitida* Poepp. & Endl.).

Theobroma sylvestre has been confused with *T. speciosum*, which is usually a larger tree, but its small axillary inflorescences, smaller, scentless and paler brown-reddish flowers, and its green-bluish fruit at maturity, distinguish it readily.

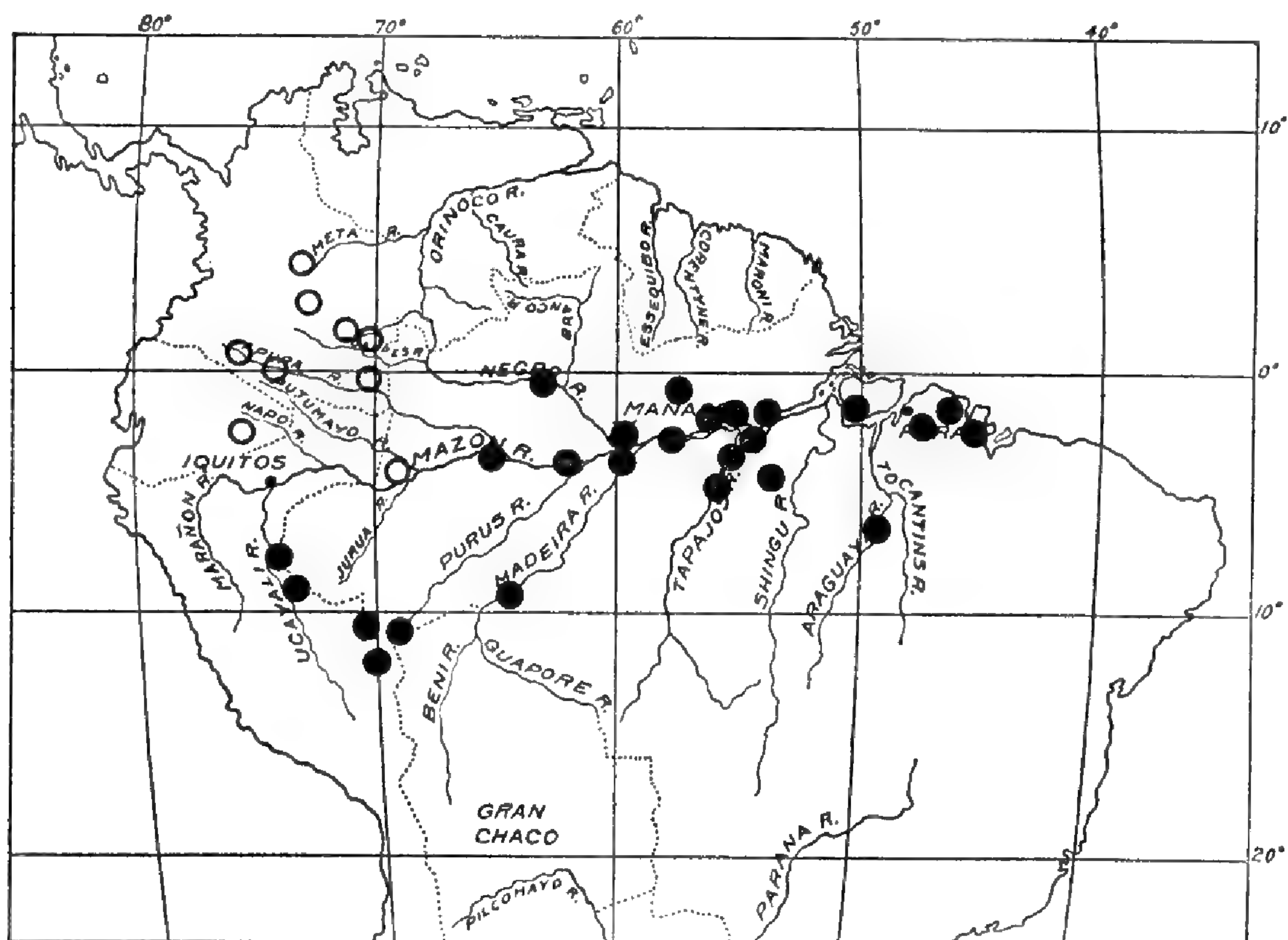
COMMON NAMES.—"Cacao azul" is generally used. Other names recorded are: Cacau azul, cacauí, cacauí, cacao-hú, cacao rana, cacau rana, cacau bravo. Cacao azul refers to the color of the mature fruit (bluish).

USES.—No special uses are recorded.

DISTRIBUTION.—More or less frequent along the Amazon River and lower part of its tributaries from Santarém to Tonantins, eastward from the mouth of the Iça. It grows on elevated ground in rather dry places, and appears frequently in secondary stands.

According to Ducke, it is common around Manaus, especially in relatively dry thickets on clay soils poor in silica.

BRAZIL: AMAZONAS: "Martius Iter brasiliensis 322: *Theobroma sylvestris* Mart. Observ. 2832, *Cacao sylvestris* Aubl., *Cacao Rana Incol.* Habitat in sylvis ad fl. Solimoes, Prov. Rio Negro," Martius [887] (Photo F. M. 40708) (M, syntype of *T. sylvestris* Mart.). "Martius Iter brasiliensis 322: *Theobroma sylvestris* Mart. in silvis ad fl. Solimoes," Martius [891] (Photo F. M. 19644) (M, lectotype). Ibidem Martius [871] (Photo F. M. 40707) (M, syntype). Ibidem Martius [888] (M, syntype). Ibidem Martius [889] (M, syntype). "Martius Iter Brasiliensis 322, in silvis ad fl. Solimoes," Martius [890] (Photo F. M. 40709) (M, type of *T. nitida*). Manaus, Mata do Aleixo, "cacaú azul," 16 III 1945, *Fróes* 20556 (IAN, NY). Manaus, Colonia João Alfredo, rain forest in noninundatable ground; small tree, flowers pale brown-rose, "cacao azul," 6 XII 1935, *Ducke* 100 (A, F, IAN, K, MG, MO, S, US). Manaus, in noninundatable forest; rather large tree with weak trunk, flowers brownish-flesh color, "cacao azul," VI 1932, *Ducke* 103 (F, Y). Manaus, matta, vicinity Igarapé da Cachoeira Grande, elevated ground; small flowers on trunk and branches, 14 X 1912, *Ducke* 12187 (G, MG). Fonte Boa, matta, elevated ground; tree 4 m., 10 cm. diam., "cacao azul," 5 IV 1945, *Fróes* 20655 (F, K, US). Ibidem, "the Indians say that it was introduced from Japura river," *Fróes* 20463 (US). "Campo experimental do I.A.N., introduced from Rio Negro, *Fróes* 34949 (IAN). Maués; small tree, flowers red, wood hard, "cacaúrana," "cacaú azul," 30 XI 46, *Pires* 136 (IAN). Rio Madeira, Rio Canumã, Borba municipality; tree 4 m., elevated ground, 12 XI 1927, *Fróes* 33788 (IAN). Rio Demei, Sumauma, Barcelos municipality; tree 8 m., fruits, flowers rose, 30 IV 1952, *Fróes* 28382 (IAN). Rio Tonantins, *Fróes* 25554 (IAN).



MAP 5.—Geographical distribution of *Theobroma speciosum* ● and *T. glaucum* ○.

PARÁ: "In vicinibus Obidos, Prov. Para, Dec. 1849," *Spruce* 166 (Photo F. M. 40702) (M, holotype and lectotype of *Theobroma spruceanum* Bernoulli; isotypes BM, WU). Obidos, "cacao azul," 7 I 1904, *Ducke* 4878 (BM, G, MG, P, US); ibidem, matta, 11 V 1905, *Ducke* 7216 (MG). Ibidem, rain forest, elevated ground; small tree, fruit green glaucous when ripe, flowers pale brownish reddish, "cacao-azul," 10 I 1920, *Ducke* 14734 (S, U). São Jorge, municipality of Faro; small tree in rain forest, flower dark red on branches, "cacau azul," 11 XI 1950, *Black & Ledoux* 50-10644 (IAN, UC, U). Oriximiná, Las Trombetas, flowers on trunk and branches, ripe fruit green, "cacao azul," "cacao-hu," 8 XII 1906, *Ducke* 7822 (BM, G, MG, US). Lazo de Faro, above Tanaenera, forest on elevated ground, "cacau azul," 12 II 1910. *Ducke* 10669 (MG). Alenquer, Estrada da Vila do Curuá, municipality of Obidos, sandy ground with vegetation of *Bertholletia* and *Attalea*; tree 2.5 m. in rain forest, 4 III 1953, *Fróes & Filho* 29465 (IAN, U). "Km 23 da BR-17 Est. a direita," firm land, sandy, natural forest; flowers yellowish red, edible fruits, 12 X 1955, "cacao bravo," *INPA (Dionisio)* 2125 (IAN).

3. *Theobroma speciosum* Willd.

FIGURES 5, 12, 13, 14, 16, 18; MAP 5; PLATES 2, 3
Theobroma speciosum Willd. ex Spreng. Syst. Veg. 3:332. 1826; Bernoulli (1869) 8, pl. 3, fig. 2; Schumann in Mart. (1886) 74; Jumelle (1899) 30, fig. 16; De Wildeman (1902) 95; Huber (1906a) 273; Ducke (1925) 130; (1940) 270, pl. 1, fig. 3, pl. 2; (1954) 13; Addison & Tavares (1951), pl. 5, fig. 2, pl. 6, fig. B, pl. 12, fig. 6; Cuatrecasas (1956) 658.

Theobroma quinquenervia Bernoulli, Uebers. Art. Theobroma 8, pl. 3, fig. 3. 1869.

Theobroma speciosum var. *quinquenervia* (Bernoulli) Schum. in Mart. Fl. Bras. 12(3):75. 1886; Jumelle (1899) 32, fig. 16; De Wildeman (1902) 95.

Theobroma speciosum var. *coriaceum* Huber, Bol. Mus. Goeldi 4:586. 1906.

Theobroma guianensis sensu Chevalier, Rev. Inter. Bot. Appl. 26:274. 1946; León (1960) 318, 319, fig., pro parte, non Gmelin.

Sapokaia brasiliensis Rich. ex Chevalier. Rev. Int. Bot. Appl. 26:275. 1946, as synonym.

TYPES.—*Siber*: "Hoffmannsegg" in Herbarium Willdenow no. 3680 (B). *Spruce* 1737, Brazil, Barra do Rio Negro (of *T. quinquenervia*). *Huber* 1567, Peru, Ucayali (of var. *coriaceum*).

Tree up to 15 m. tall; trunk about 20 cm. in diameter with light gray, smooth bark; sympodial growth by lateral, subterminal upright shoots; primary branches ternate, usually furcate, spreading; branchlets terete, smooth, more or less pulverulently stellate-pilose, later glabrate, grayish brown; crown rather narrow; stipules subulate, short, stellate-tomentose, soon deciduous.

Leaves firmly coriaceous, distichous; petiole robust, subterete, densely stellate-tomentulose, 8-14 (-20) mm. long, 2-4 mm. thick; blades usually large, ovate-oblong or elliptic-oblong, broadly rounded or very obtuse and asymmetrical at base, exceptionally (in orthotropic branches) cuneate and symmetrical, attenuate near the apex, abruptly and acutely acuminate, the margin entire or very slightly sinuose, often slightly revolute, 20-40 cm. long, 7-18 cm. broad, the

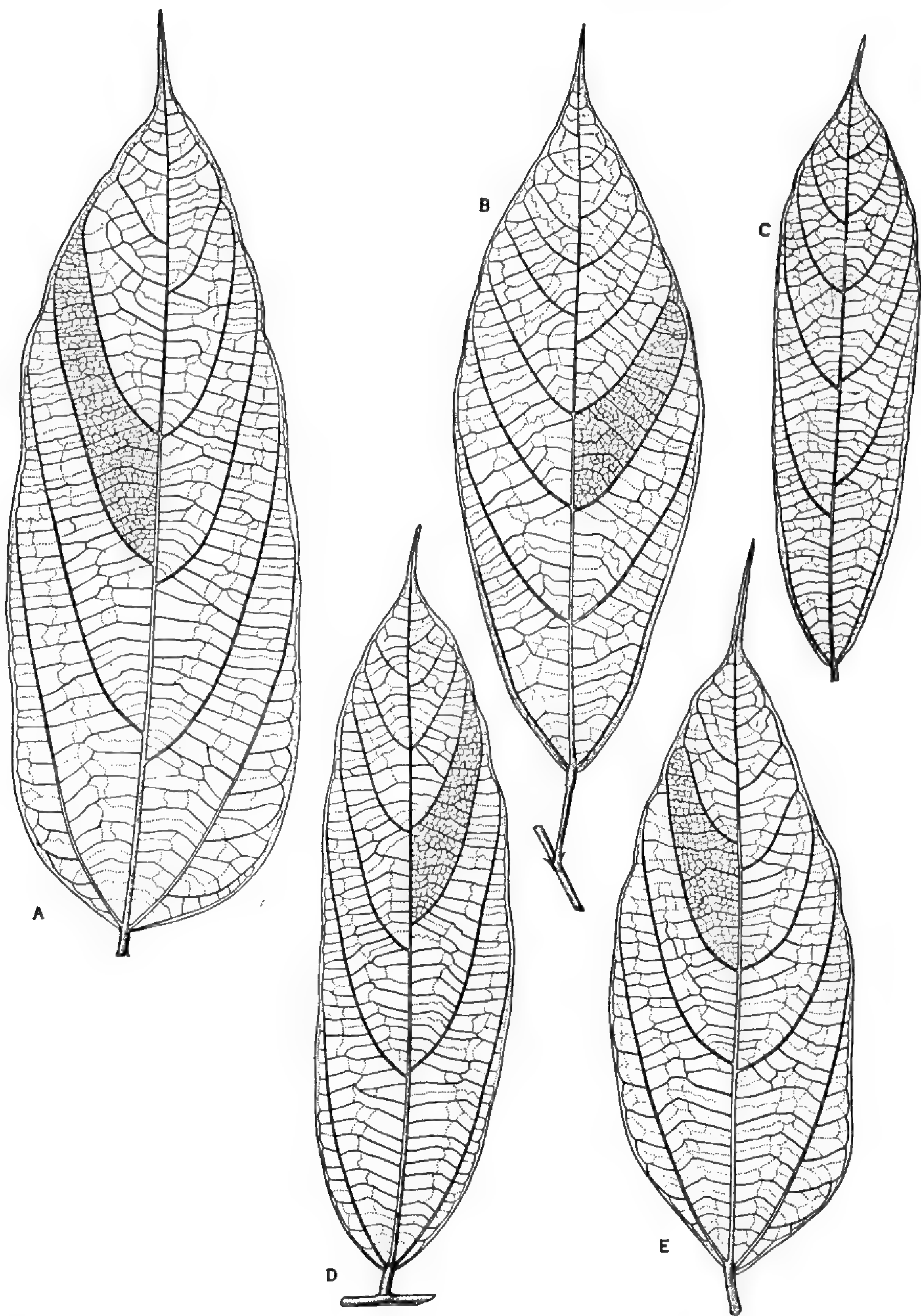
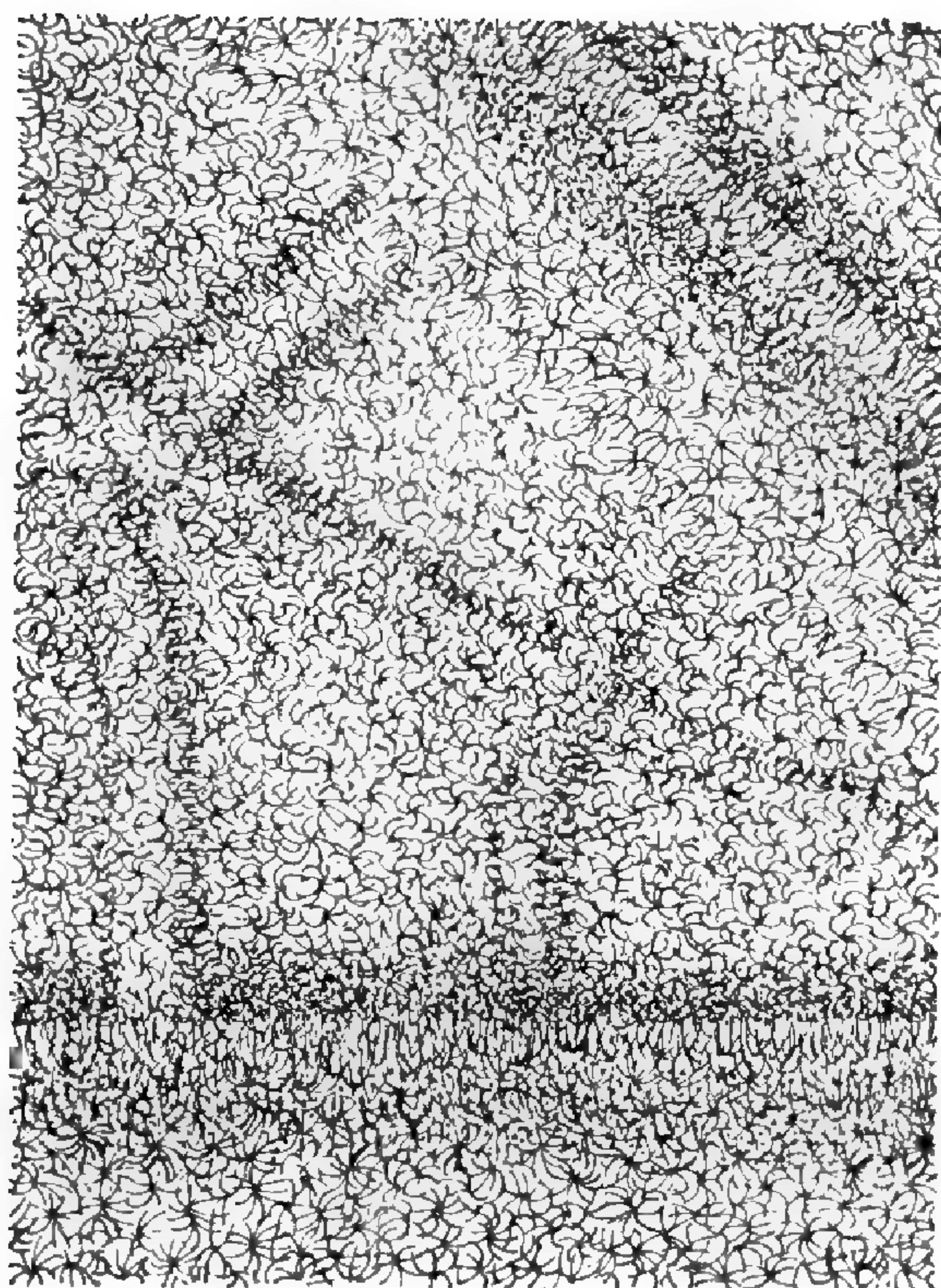


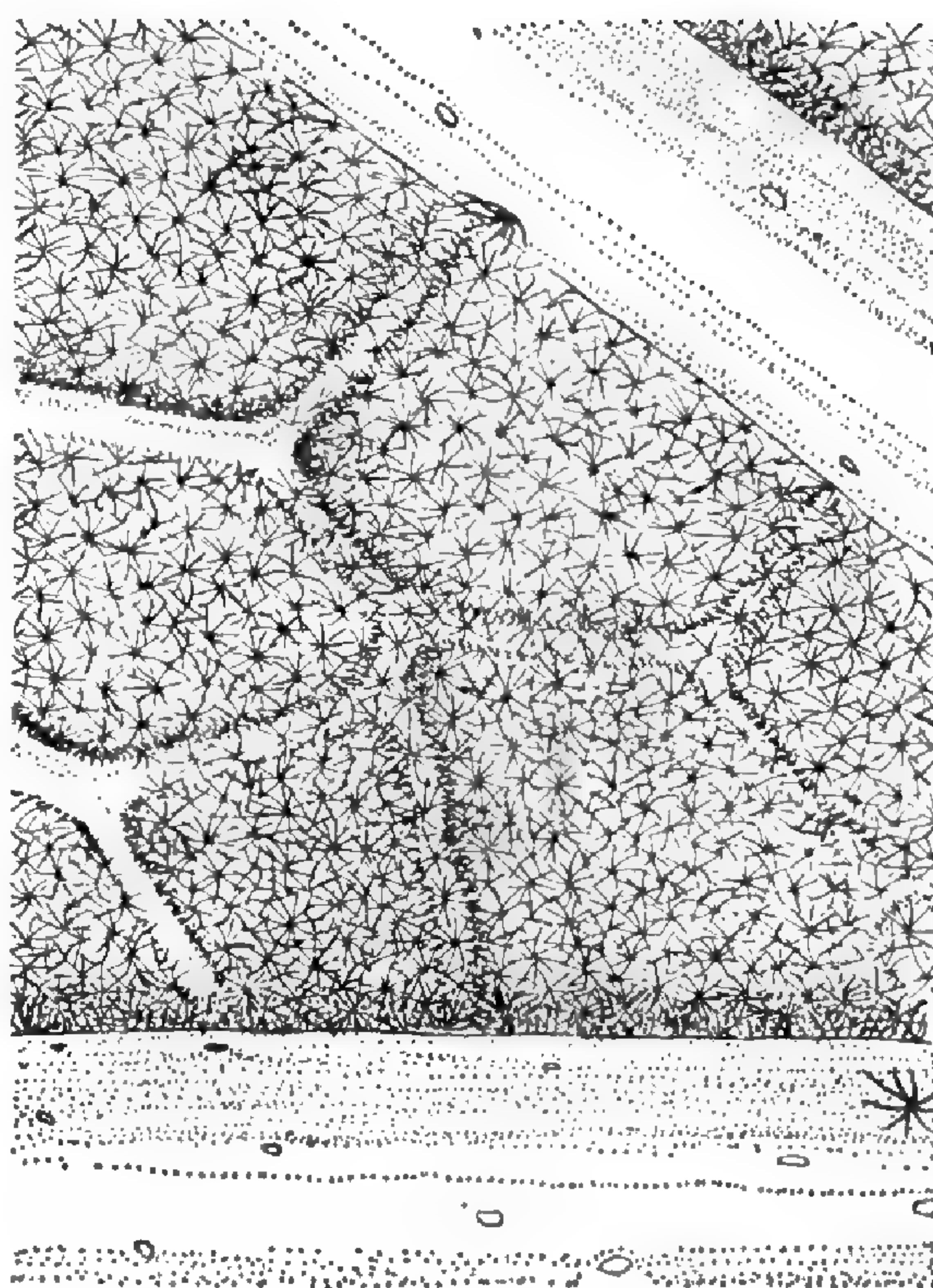
FIGURE 17.—Leaves of *Theobroma*, $\times \frac{1}{3}$: A, *glaucum*, from lateral branches (Bartley & Holl. 74); B, *glaucum*, from orthotropic branches (Baker 37); C, *bernouillii* subsp. *asclepiadiflorum* (Wedel 681); D, *bernouillii* subsp. *bernouillii* (Pittier 3199); E, *bernouillii* subsp. *capilliferum* (Cuatr. 16160).

acumen 1.5–2.5 cm. long; lustrous above, green, usually pale brown or olivaceous when dry, glabrous, or with a few stellate hairs on the nerves, the costa and main nerves filiform, conspicuous, the minor veins less noticeable or obsolete, pale cinereous beneath with tawny nervation, the costa thick, very prominent, the 6–8 pairs of secondary nerves prominent, subcurvate ascending, near the margin thinner, curving, decurrent and anastomosing, the inferior pair stronger, forming together with the midrib a trinerved base, the transverse tertiary nerves thin but prominent, 5–15 mm. distant from each other, sometimes the basal more conspicuous, forming together with main nerves a basally 4- or 5-nerved leaf; minor veins prominulous, reticulate; main nerves glabrous or subglabrous with sparse, stellate hairs and scattered callose dots, the tertiary glabrous or subglabrous, the minor reticulate veins and the areoles covered by dense minute whitish sericeous tomentum of stellate hairs.

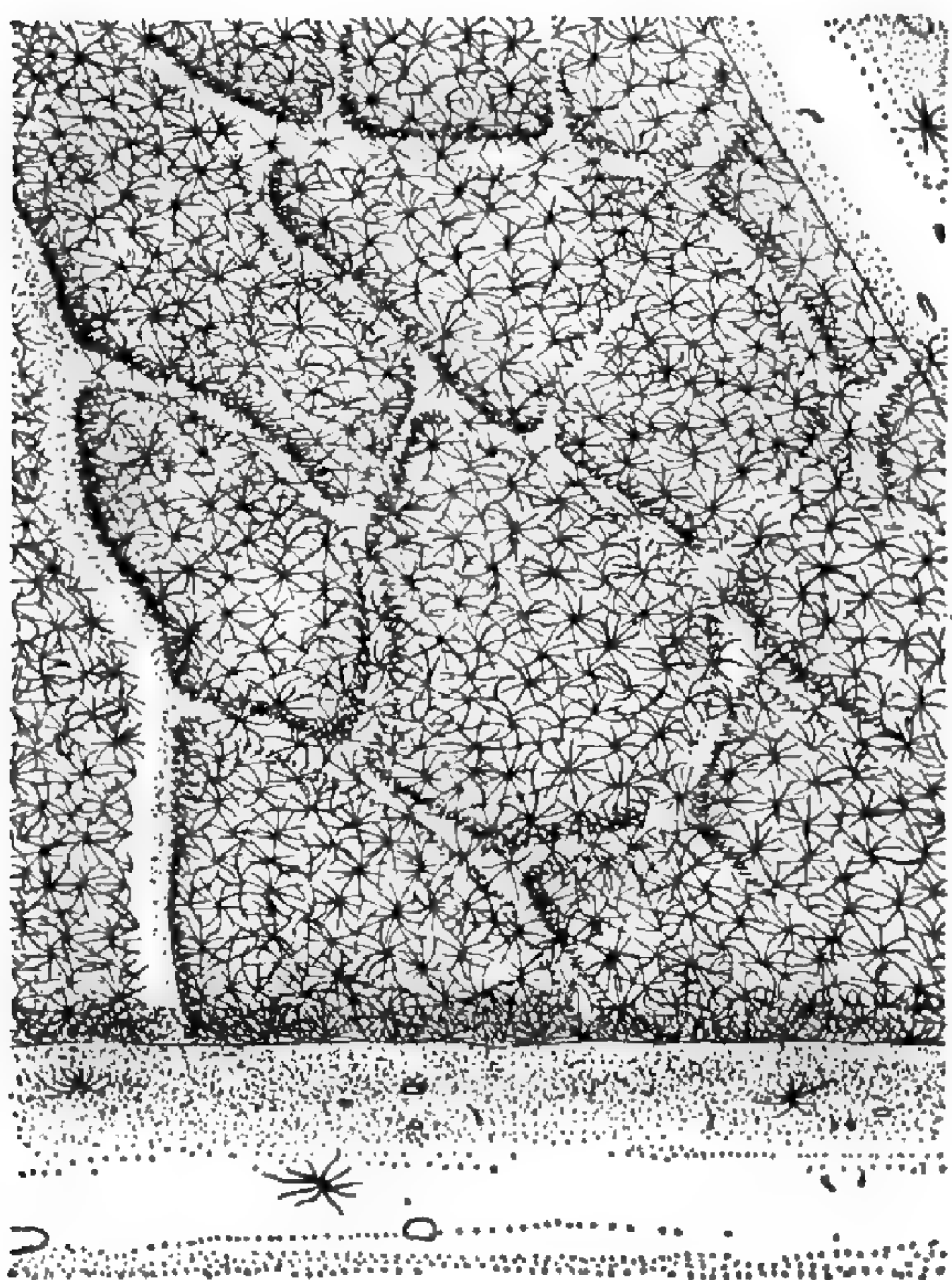
Inflorescences on trunk, forming delicate panicles gathered in many-flowered bunches borne on woody, short, tuberculose branches, often very showy with up to 250 dark-red or purplish-red fragrant flowers; panicles 3–10 cm. long, dichotomously furcate-branched from the base, the branches thin but rigid, reddish and covered with a minute, whitish tomentum, the terminal branchlets (peduncles) thin, flexuous, 10–25 mm. long, 3-bracteolate and articulate to the pedicel at apex; pedicels slender, 5–20 mm. long, minutely tomentulose; bracteoles minute, linear or linear-triangular, 1–2 mm. long, 0.2–0.5 mm. wide, very soon deciduous; buds ovoid, 7–9 mm. high, rather reddish, with 5 longitudinal, white-tomentose, prominulous commissural lines, sparsely stellate-pilose; sepals rather thick, oblong, subobovate-oblong, attenuate toward the base, abruptly narrowed and subobtuse at apex, the margin incurved with a minutely, whitish tomentulose strip inside, the apex shortly cucullate-inflexed, the inside purplish and glabrous, except for glandular trichomes at base, the outside sparingly stellate-pilose, usually one free and the others united one third or almost completely by pairs, 10–12 mm. long, 3.5–4 mm. broad; petal-hoods thick-membranaceous, trinervate, whitish with red lines, oblong-obovoid, attenuate-clawed at base, rounded cucullate at apex, with sparse, thin, spreading hairs outside, 6–7 mm. long, about 4 mm. broad; petal-lamina rather thick, red or dark red, transversely elliptic, subtruncate, slightly emarginate and mucronulate at apex, abruptly cuneate-attenuate at base, entire or slightly erose at margin, conspicuously (especially by transmitted light) reticulate-veined, 5–7.5 mm. long, 7–9 mm. broad; androecium tube thick, about 2–3.5 mm. high, sparsely stellate-pilose; staminodes purplish red, subulate, thick, the apex thinner and curled, minutely muricate-pilose, 5–7 mm. long, 1.2–1.8 mm. wide; filaments glabrous,



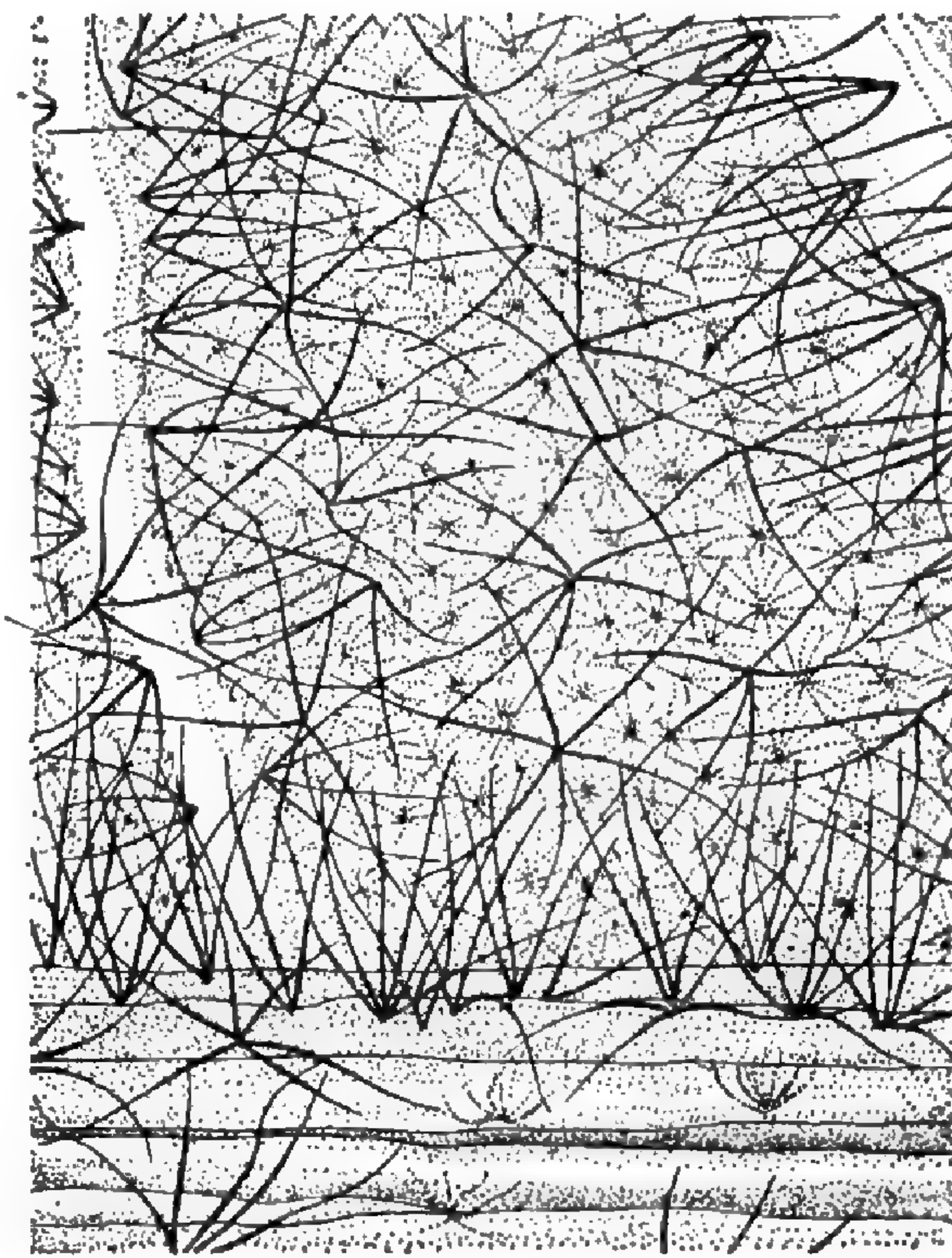
A



B



C



D

FIGURE 18.—Indument on the underside of leaf in: A, *Theobroma bicolor* (Killip & Smith 30006); B, *T. sylvestre* (Ducke 100); C, *T. speciosum* (Ule 9629); D, *T. velutinum* (Benoist 516). A, B, and C $\times 30$, D $\times 20$.

about 2 mm. long, curved, dilated at base, minutely 3-furcate at apex, triantheriferous; anther lobes ellipsoid, about 0.4 mm. long; ovary ovoid-ellipsoid, 2–3 mm. long, 5-ridged, whitish velvety-tomentose; styles 5, subfiliform, 1.2–2 mm. long, glabrous, connivent, only united at base.

Fruit globose-ellipsoid, about 10 cm. long and 7–8 cm. broad, almost smooth, with 5 more or less conspicuous (when dry depressed) costae, shortly and densely tomentose-velvety, yellow when ripe; pericarp about 5–6 mm. thick, the inner layer coriaceous, smooth, very hard, about 0.5–1 mm. thick, the middle tissue about 3–4 mm., carnose, the outer layer coriaceous but less hard than the innermost and becoming rugose after the shrinking of the intermediate layer by drying; seeds about 20–26, surrounded by whitish, sweet, scentless pulp, ovoid-oblong or ellipsoid-oblong, 24–26 mm. long, 13–14 mm. broad, 10–12 mm. thick, the episperm thick (about 1 mm.), coriaceous with the middle layer becoming gelatinous; embryo white, oblong, covered by a very thick pellicle, 22–24 mm. long, 10–11.5 mm. broad, 9–10 mm. thick; germination epigeous.

The leaves of the type of *T. speciosum* are long-petiolate, cuneate and trinerved at the base. *Theobroma quinquenervium* Bernoulli was described from a specimen with short-petiolate, broadly oblong leaves, asymmetrically rounded at the base. In the first type the margins of the leaves are close and parallel to the prominent, basal pair of secondary nerves; in the second the margins of the leaves are broadened and remote from the prominent basal pair of nerves, and an additional lower tertiary nerve on each side makes the base of the blade somewhat 5-nerved. The latter type of blade, borne on a short, stout petiole, is the common one in the species. Leaves with slender, long petioles, thickened at both ends, and cuneate blades are seldom found; they appear on young, orthotropic terminal branches. This dimorphism was already noticed by Huber who first united *T. quinquenervium* and *T. speciosum*.

The type specimen was collected near Belém de Pará by Siber who was sent on a collecting trip to Brazil by Hoffmannsegg; it is preserved in the Berlin-Dahlem Botanical Museum in the Willdenow Herbarium. I have been able to study this specimen thanks to the kindness of Prof. Werdermann and Prof. Melchior. The photograph F.M. 9640 is from a specimen at B now destroyed, which agrees perfectly with the type in the Willdenow Herbarium, of which it was undoubtedly a duplicate. In his monograph, Chevalier made this species a synonym of *T. guianense* (Aubl.) Gmel., but this is a confused species, the identity of which is discussed in this paper.

Spruce and Ducke called attention to beauty of this tree in blossom, according to Spruce "one of the prettiest things I have seen."

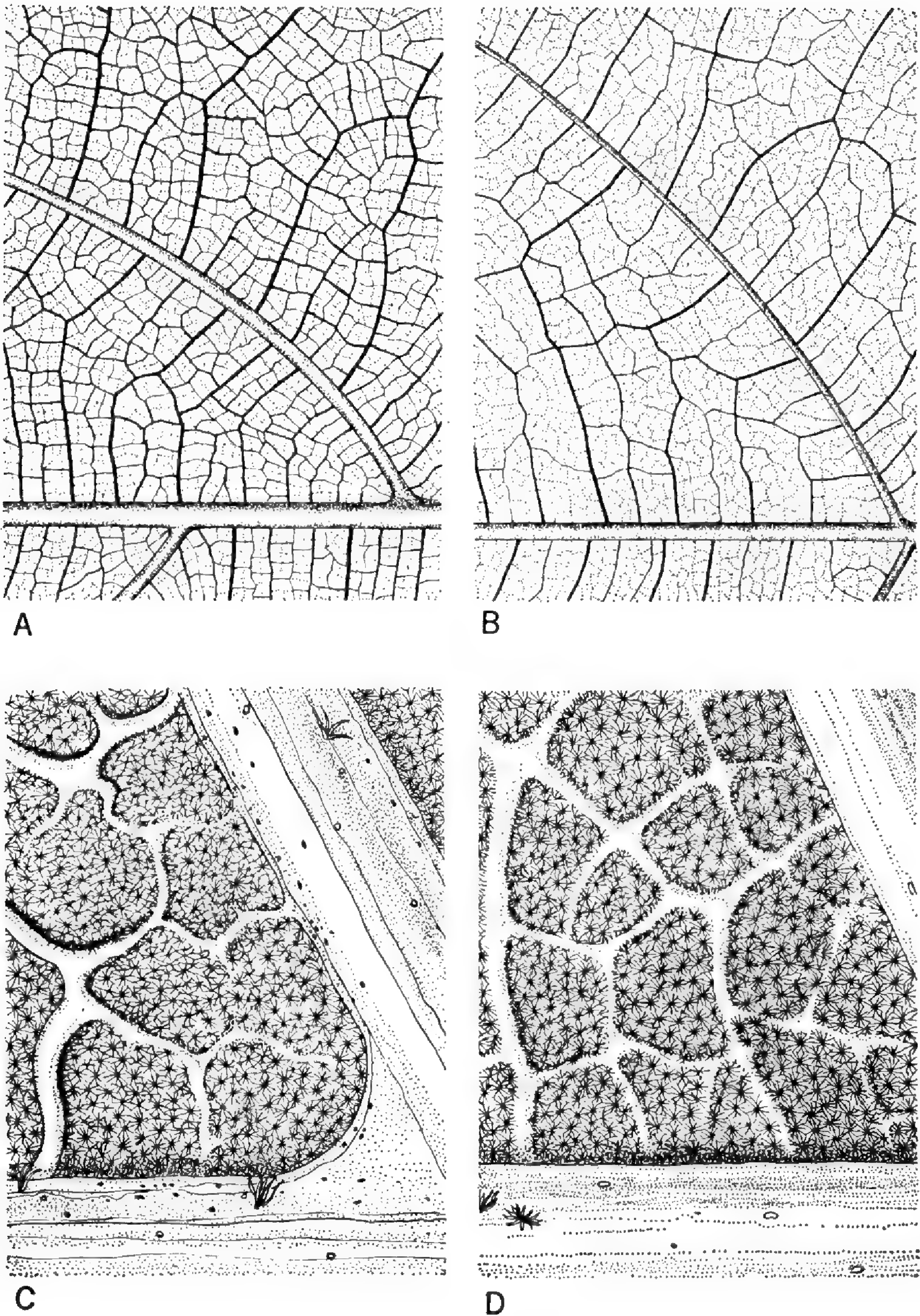


FIGURE 19.—A, B, Detail of nervation at the underside of the leaf in: A, *Theobroma speciosum* (Ule 9609); B, *T. cacao* (Cuatr. 7756). C, D, indument on the underside of the leaves in: C, *T. glaucum* (Bart. & Holl. 74); D, *T. bernouillii* subsp. *capilliferum* (Cuatr. 16160). A and B $\times 2$, C and D $\times 25$.

Theobroma speciosum can grow to be 15 m. high, with a few whorls of dichotomous leafy branches near the top of a long branchless stem, which can bear abundant, large, cauline inflorescences. These may form large cushions of showy, blood-red, wine-red, or purplish-red flowers which give off an intense lemon- or orange-skin odor (Ducke). The outer pulp of the seeds is sweet but scentless. It is said to be easy to grow in gardens.

COMMON NAMES.—Cacauí, cacauu. Other recorded names or different ways of spelling are: cacao-y, cacao-u, cacau, cacaohy, cacau-i, cacao-i, cacaoillo, cacau-rana, cacao-rana, cacao biaro, cupuy, cupuyh, cacao do matta, cupurana, cacao azedo, cacao sachá (Peru), chocolatillo (Bolivia).

USES.—The pulp is eaten by natives. The seeds are used very occasionally to prepare low quality chocolate.

DISTRIBUTION.—This species extends throughout the Amazoniã Hylaea except in the northwestern section, from the state of Maranhão at Cururupu to Acre and Madre de Dios in eastern Bolivia and the Ucayali River (Loreto) in Peru. It grows on noninundatable ground in rain forests as well as in not too humid places and it appears also in secondary growth near towns, but it is never of frequent occurrence.

BRAZIL: "Bresil. Herb-Lusit," "*Herrania paraensis*," "*Theobroma subincanum* Mart.?" *Geoffroy* [St. Hilaire?] s.n. (P). "Polyadelphia Decandria *Theobroma speciosa* foliis acuminatis integerrimis subtus tomentosus. Flores purpurei. Habitat in Para Brasilia," "*Theobroma speciosa* (W.) Spreng. Bernoulli determ." *Hoffmannsegg*, W. (B, Herb. Willdenow 3680, holotypus). "Ex herb. Linn. *Theobroma speciosa* Brasil Col." *Siber* (B), specimen destroyed (photograph F. M. no. 9640); identical with the type in the Willdenow Herbarium.

PARÁ: Belém, noninundatable forest near city; small tree with dark-red flowers on trunk, "cacaohy," IX 1936, *Ducke* 281 (A, F, K, MO, NY, S, US). Belém, Jardim Botânico do Museo Goeldi; slender tree, inflorescence on trunk, petals dark red, sepals reddish stained, fruit 5-parted, yellow when ripe, "cacau-i," 26 VIII 1942, *Archer* 7619 (IAN, K, NY, USDA). Ibidem, slender tree, "cacao-i," 29 X 1942, *Archer* 7721 (IAN, USDA). Ibidem, small tree, flowers deep crimson, calyx light pink, leaves deep green above, gray green beneath, cultivated, 15 VII 1946, *Schultes & Silva* 8066 (GH). Ibidem, 19 X 1945, *Pires & Black* 695 (IAN), 740 (IAN). Bragança, "cacao claro," XII 1899, *Huber* 1748 (G, MG). Taperinha, at Santarém, secondary forest on elevated land; small tree, red flowers on trunk, "cupuy," *Ginzberger* 802 (WU). Rio Curuauna, Cachoeira do Portao, region of Planalto de Santarém, rain forest, XI 1954, *Fróes* 31414 (IAN). Santarém, hills, "cacao do Matto," *Jobert* 903 (P). Near Obidos, Prov. Pará, XII 1849, *Spruce* s.n. (K, Herbarium Hookerianum 1867). Forest near Obidos, XII 1845; slender tree 40-50 ft., flowers on the naked stem, leaves on the top of the tree only, "cacao-rana," *Spruce* 456 (K, Herbarium Benthamianum, 1854, P, BM). Monte Alegre, region of Colonia da Mulata, elevated ground; tree 8m., red flowers, 28 IX 1953, *Fróes* 30432 (IAN). Breves, VII 1956, *Pires, Fróes, & Silva* 5886 (IAN). Belterra, capoeira, way to Pindobal; tree 7 m., red flowers on trunk with lemon scent, leaves white beneath, 31 XI 1947, *Black* 47-1889 (IAN, NY). Region Tapajós, Boa Vista firm land; tree 4 m.,

10 cm. [diam.], flower color wine, fruits on the trunk, eaten by Indians, "cupuhy," 30 VIII 1932, *Capucho* 397 (IAN, F). Tapajós, Vila Braga; tree, dark-red flowers borne on the trunk, 27 X 1908, *Snethlage* 10044/b (MG). Upper Cupary River, plateau between the Xingú and Tapajós Rivers; tree 25 ft. high, 2 inches in diam. breast high, in high forest, flowers red on old wood, "cacaorana," IX 1931, *Krukoff* 1117 (A, G, K, NY, P). Ibidem; tree near river shore; flowers dark red, borne on large branchlets; wood used for "farinha" containers (to keep it dry), "cacaorana," *Krukoff* 1080 (A, BM, G, K, MICH, MO, NY, S, U). Rio Cumina-mirim, forests at NE; ripe fruit yellow, only on trunk, "cacaorana," 16 XII 1906, *Ducke* 7975 (MG). Oriximina, Las Trombetas, "cacao rana," flowers only on trunk, 8 XII 1906, *Ducke* 7884 (G, MG).

AMAZONAS: Near Barra, Prov. Rio Negro, Aug. 1851; forests south of Rio Negro; tree 20 feet, straight with a whorl of branches only at summit, which are twice or thrice dichot[omous]; trunk almost completely clad with flowers, which have fine odor of bruised orange leaves; petals cucullate, claw pink, white limb dull crimson with dark veins. The subul[ate] processes blood red; one of the prettiest things I have seen, *Spruce* 1737 type of *Theobroma quinquenervium* Bernoulli (M, holotype, Photo F. M. 40703; isotypes: BM, E, F, G, GH, GOET, K, LD, LE, OXF, P, WU) (Photo F. M. 9639 from Berlin). Rio Marmellos, near mouth; flower deep salmon red, buds dark crimson, bark smooth, light gray white, leaves pale dull beneath, dark green glossy above, branches umbelliform at top, trunk 6-7 inches in diameter at base, 20-22 feet tall, inflorescences 200-flowered; seeds give low grade chocolate, 2-12 VIII 1945, "cacao azedo," *Schultes & Cordeiro* 6507 (AMES, F, IAN). Amazonas, Rio Capitare, municipality of Codajas, elevated ground, high forest; tree 8 m., red flowers, 3 IX 1950, *Fróes* 26526 (IAN). Manaus, Estrada do Aleixo; tree 5 m., fruits on trunk, 14 V 1953, *Fróes* 30180 (IAN).

GUAPORE: Porto Velho, Estrada de Rodagem, Km 8, Viana, disturbed forest, elevated land; small tree, red flowers with lemon scent, 31 V 1952, *Black, Cordeiro, & Francisco* 52-14655 (IAN).

GOIAS: Margem do Rio Araguaia; tree 4 m., red flowers, 13 VI 1953, *Fróes* 29732.

ACRE (TERRITORIO DEL): Rio Acre, Seringal San Francisco; tree 5-20 m., black-purplish flowers on stem, VII 1911, *Ule* 9609 (G, K, L), *Ule* 14448 (MG). Near mouth of Rio Macauhan (tributary of Rio Yaco), Lat. 9°20' S., Long. 69° W., on firm land; tree 40 feet high, 5 VIII 1933, *Krukoff* 5295 (A, F, K, LE, M, MICH, MO, NY, S, U, UC, US).

RIO DE JANEIRO: Quinta de Sao Christovas, 10 I 1876, *Glaziov* 9633 (C, P). Jardim Botânico, flowers on trunk and main branches, V 1944, *Camargo* 2395 (IAN).

PERU: LORETO: Region of the middle Ucayali, rain forest, Yarina Cocha, 155 m. alt., elevated ground; tree 12-15 m., 35 cm. thick, the first branch at 7 m. from ground, flowers with strong anise scent, sepals red crimson, petals dark crimson-striped on white ground, stamens less crimson than petals, pistil whitish, "cacao sachá," 22 IX 1925, *Tessmann* 5398 (G, M, S). Rio Ucayali, Paca, 21 VII 1898, *Huber* 1567 (Holotype of var. *coriaceum* Huber, MG; isotypes BM, US), (photo F. M. No. 1567). 40 km. south of Pucallpa, rain forest of the Amazon basin virgin rain forest on loamy sand, *Ellenberg* 2565 (U).

BOLIVIA: Km. 7 on road Guayaramerin-Cochuela Esperanza, [Prov. Vaca Diez, Depto. Beni], 120 m. alt., "chocolatillo"; growing wild in rain forest; flowers wine red, borne on cushions along the whole, rather slender trunk, dichotomous branches slender, pendent, fruits small. I have seen also a specimen in Brasilia, where it is called "cacau-i"; 9 IX 1954, *Patiño* s.n. (GH). Junction of Rivero

Beni and Madre de Dios; pulp edible and equal to that of *T. cacao*, seeds white, not used, VIII 1886, *Rusby* 654 (BM, E, F, G, GH, K, LE, MICH, MO, NY, P, US). Unduavi, 10,000 ft., *Rusby* 647 (US).

4. *Theobroma velutinum* Benoist, Bull. Mus. Hist. Nat. Paris **27**: 113. 1921.
FIGURES 3, 12, 13, 14, 16, 18; MAP 1.

Herrania guianensis Sagot ex Schum. in Mart. Fl. Bras. **12**(3): 75. 1886.

Theobroma speciosum sensu Uittien in Pulle, Fl. Surinam **3**: 45. 1932.

Theobroma sp. 4, Uittien in Pulle, Fl. Surinam **3**: 46. 1932.

Herrania guyanensis Sagot in Chevalier, Rev. Int. Bot. Appl. **26**: 275. 1946
(as synonym).

TYPE.—*Benoist* 516, French Guiana.

Branches terete, subcinereous, densely appressed stellate-tomentose or becoming glabrate, grayish brownish; branchlets densely tomentose.

Leaves large, firmly coriaceous; petiole robust, subterete, densely appressed cinereous-tomentose, when old transversely rimose, 12–14 mm. long; lamina oblong-ovate or ovate-oblong, broadly rounded and more or less asymmetrical at base, suddenly narrowed and long-acuminate at apex, the margin slightly revolute, entire or very slightly sinuose, 28–40 cm. long, 16–21 cm. broad, including the acumen, this about 3 cm. long, pale olivaceous above (when dry), subnitidous, slightly and broadly bullate, glabrous except for the midrib, this sparsely pilose towards the base, the costa and secondary nerves thin, the tertiary nerves filiform, the minor veins less apparent or obsolete, softly velutinous beneath, ochraceous-cinereous, the midrib very prominent, the 5–7 pairs of secondary nerves prominent, ascending, curved near the margin and anastomosing, the longer pair stronger, more separated from the next, the transverse tertiary nerves prominent, others broadly reticulate, prominulous, the lesser veins forming a minute, prominulous reticulum, the minor reticulum and its areoles densely tomentose with minute, white, dense, subappressed, stellate hairs, the other nerves and the sides of the midrib covered with abundant, long, delicate, stellate hairs with long, thin, spreading rays.

Inflorescences many-flowered, borne on lignose, tuberculate branches on the trunk, the panicles fasciculate, ramose from the bases, 5–12 cm. long, the branchlets moderately thin, cinereous, hirtellous-tomentellous with thin, mediocre, stellate hairs, the terminal (peduncles) thinner with 2 or 3 deciduous bracteoles at the end; pedicels slender, 6–18 mm. long; bracteoles at the joints minutely lanceolate, hirtellous, deciduous, 1–1.5 mm. long; sepals thick-membranaceous, spreading, shortly united at base, lanceolate-oblong, subacute, glandular at base, otherwise glabrous inside, with fine stellate hairs copious on the outside, the margin minutely tomentulose, about 10 mm. long and 3.5–4.5 mm. broad, usually one free, the others united by pairs. Petal-hoods 6–7.2 mm. long, about 3 mm. broad, membranaceous, obovate-oblong, cucullate-rounded at apex, 3-nervate, the median

vein furcate, outside sparsely, weakly pilose, the end auriculate-emarginate, articulate to the erect lamina, 6–7.2 mm. long, about 3 mm. wide; petal-lamina sessile, subtrapezoid, subtruncate or often slightly sinuate or 3-toothed at apex, abruptly narrowed into a short claw at base, moderately thick, but venation conspicuous by transmitted light, glabrous, somewhat rugulose-papillose toward the base, 5 mm. long, 6–6.5 mm. broad; androecium-tube about 2 mm. long and 2.4 mm. broad, minutely papillose-pilose; staminodes purplish red, lanceolate-subulate, thick, suddenly narrowed into a short, crisp, acute acumen at apex, minutely muricate-pilose, about 6 mm. long and 1.5 mm. wide; filaments triantheriferous, 2.5 mm. long; ovary ovoid-oblong, about 2.2 mm. long, 5-ridged, tomentose; styles 5, connivent, adherent, easily separable, glabrous, 2 mm. long.

Fruits ellipsoid, densely and softly stellate-pilose-velutinous, 5-costate, the ribs thick, very prominent, the surface smooth, 8.2–9 cm. long, 6–6.3 cm. broad, the pericarp 3–4 mm. thick; seeds usually 25–30 in each pod.

This species is closely related to *T. speciosum*, having very similar flowers and leaf outline. However, *T. velutinum* is very different on account of the structure of the fruits and the indument. The ellipsoid, densely velvety fruits have 5 longitudinal, very prominent, typical ribs, a character only known in this species. The leaves beneath have a soft, velvety indument of long, thin, stellate or dendroid, more or less densely distributed hairs on the whole nervation and a lower layer of a short, dense tomentum of minute, stellate, intricate hairs covering the areoles and the minor reticulate veins. Also, the terminal branches are densely tomentose and the inflorescence branchlets and pedicels have copious, rather long, fine hairs.

Theobroma velutinum is only known from French Guiana and the neighboring Dutch side of Maroni River valley. The excellent foliage and fruiting collections made by Benoist and recent other collections by members of French and Dutch Forest Services, especially the flowering specimens B. B. S. 1161, have facilitated a complete description of the species. Its inflorescences are cauline, many-flowered, and often showy, like those of *T. speciosum*. The Sagot collection 1206, preserved in several herbaria and consisting only of large inflorescences, belongs to this species. Sagot named it *Herrania guianensis* and left an accurate unpublished description which is attached to the specimens in Paris.

COMMON NAMES.—Bouchi-cacao, cacao sauvage, cacao.

USES.—Reported to yield edible seeds comparable to cacao but no information is given on the quality of the product.

DISTRIBUTION.—French and Dutch Guiana in the valley of Maroni River.

SURINAM: 4 X 1950, B. W. 1161 (U). Placer l'Arver, 31 X 1918, *Gonggryp* 4108 (U). Flur of Marowyne, Reu naar L. etwa en Tupanahoni, No. 47 Marowyne, 26 XI 1918, *Gonggryp* 4127 (U). Flur Tapanahoni, III 1922, No. 33 Tapanahoni, *Gonggryp* 4148 (U).

FRENCH GUIANA: A 1 kilometre plus ou moins du camp de transportés de Charvein, le long de chemin qui conduit a la leproserie de l'Acarouany, 8 I 1914, *Benoist* 516 (P, holotype, foliage and fruits). Crique Serpent, rive droit à 1 kilometre de la crique terrain en pente, à proximité immédiate d'un ravin rocheuse; arbuste ayant été repéré au moment de sa fructification en février 1951; abattu depuis et pourvu de rejets de 3 m. de haut; produit de gousses côtes contenant des grains comestibles, "bouchi cacao" (*Paramaka*), 12 XII 1952, BAFOG 136M (P). Placean No. 2, Carreau No. 3, route de mana, terrain sablonneux; fruits jaunâtres, gousses ovoïdes de 7 à 8 x 10 à 12 cms. déhiscents, sparses sur le tronc de l'arbre, "bouchi cacao," "cacao sauvage," 19 III 1956, BAFOG 7386 (P). Karouany, 1858, "Flores atropurpurei suaveolentes, fructus ovatus, pentagonus, breviter tomentosus cacao sativa paulo minor, folia non vidi, flores e ligno prodeunter, "cacao," "*Herrania guianensis* Sagot," 1858, *Sagot* 1206 (BM, G, K, P, U, WU); type of *Herrania guianensis* Sagot (only inflorescences and flowers in all the specimens; a long and accurate description made "in vivo" by Sagot is attached to the specimens at Paris).

5. *Theobroma glaucum* Karst.

FIGURES 2, 10, 14, 16, 17, 19; MAP 5; PLATE 4

Theobroma glaucum Karst., *Linnaea* 28:447. 1856; Triana & Planch. (1862); Bernoulli (1869) 10; Jumelle (1899) 34; De Wildeman (1902) 97; Chevalier (1946) 277.

Theobroma calodesmis Diels, *Notizbl. Bot. Gart. Berlin* 14:336. 1939; Baker, Cope & al. (1954), *figs. 10, 12*; Cuatrecasas (1956) 655; León (1960) 314, 317, *fig.*

YPES: *Karsten* s.n. Colombia, San Martín. *Schultze-Rhonhof* 2312, Ecuador, Papayacu (of *T. calodesmis*, formerly in Berlin).

Tree 8–15 m. high; stem up to 30 cm. in diameter, with grayish, inside reddish bark and white wood; sympodial growth by lateral, subterminal, upright shoots; primary branches ternate, regularly dichotomous, spreading, deciduous when old, the terminal minutely stellate-pulverulent with additional simple, spreading hairs, soon glabrate, smooth, rather shining, dark brown or somewhat purplish; stipules linear-subulate, 4–5 mm. long, sparsely stellate-pilose, soon deciduous.

Leaves coriaceous, rather rigid, distichous; petiole robust, densely ferruginous or brownish tomentose with stellate hairs, transversely rimose when dry, 0.8–1.8 cm. long; blades oblong-ovate or ovate-oblong, broad in the lower third, obtusely cuneate at base, narrowed near the apex, prolonged with a long slender appendage, the margin entire or slightly sinuate and slightly revolute, 16–36 cm. long, 7–13 cm. broad, the acumen 2–3.5 mm. long, shining above, green, pale olivaceous brown when dry, apparently glabrous but with sparse mediocre stellate hairs and callose scar-dots on the nerves, the costa and secondary nerves prominently filiform, the others slender, more or

less noticeable, somewhat cinereous beneath, glaucous or pale rosy, with a glabrous aspect but the rather shining, pale brownish principal nerves sparsely callose-dotted and with very scarce ferruginous, stellate hairs, the small veins glabrous, the areoles covered with a very appressed microscopic tomentum of minute, white, stellate hairs, the costa very prominent, the 4 or 5 pairs of secondary nerves prominent, the basal one at an acute angle (remote from the margin), ascending, the others curved-ascending, near the margin becoming slender, decurrent, curving, anastomosing, the cross-tertiary nerves thinner, prominent, 3–10 mm. distant from each other, the lesser veins minutely prominulous-reticulate; leaves of the orthotropic spreading-puberulous branches long-petiolate, with the blades attenuate-cuneate at base, the lower pair of nerves very close to the margin, the petiole slender, 3.5–4 cm. long.

Inflorescences on the trunk, often many-flowered and showy, with up to 200 flowers, the base woody-tuberculate; branches 3-many, mediocre, 4–6 cm. long, furcate-ramose from near the base, the branchlets fastigiate, angulate, rather rigid, ferruginous-tomentose, the terminal (peduncles) moderately robust, 3–4 mm. long, articulate to pedicel, this 5–15 mm. long, striolate, slightly thicker, tomentellous, the subtending bracteoles minute, ovate-lanceolate, about 1 mm. long, very soon deciduous; buds ovoid, round at base, subacute at top, densely stellate-tomentose, 8–9 mm. long, about 6 mm. broad.

Calyx umbilicate; sepals thick, lanceolate-oblong, acute, inflexed at apex, connate for 2 mm. at base, densely and appressed stellate-tomentose outside, within minutely, whitish stellate-pilose near the margin and glandular at base, otherwise subglabrous, 12–13 mm. long, 3.5–4 mm. broad, curved-spreading after anthesis.

Petal-hoods light red, oblong-obovate, shortly unguiculate at base, rounded cucullate at apex, the end emarginate, biauriculate, articulate to the lamina, the 3-nerves prominent inside, thin, with spreading, weak, sparse hairs outside, 5–6 mm. long, 2.5–3 mm. broad; petal-lamina red crimson, thick, minutely rugose, and more or less translucent-venulose, glabrous, suborbicular or broadly elliptic, subsessile at base, abruptly contracted into a short claw, minutely sinuate at margin, 5.5–7 mm. long, 5–6.5 mm. broad, the claw 0.5 mm. long.

Staminal tube about 2 mm. high and 2.5 mm. in diameter; staminodes red crimson, erect, lanceolate-subulate, acute at apex, fleshy, minutely muricate-pilose, 10–12 mm. long, 1.4–1.8 mm. wide above base; filaments flexuose, 2.5–3 mm. long, glabrous, shortly 2 or 3 furcate at apex, bearing 2 or 3 anthers, the loculi ellipsoid, convergent, 0.5–0.6 mm. long; ovary oblong, about 2 mm. long, 5-ridged and sulcate, hirsute-tomentose; styles connivent, 3 mm. long, united only at base.

Fruits ellipsoid-oblong, obtusely pentagonal, broad and umbilicate at base, more or less attenuate and subacute at apex, the pericarp 1 cm. thick, coriaceous, rigid, densely and minutely velutinous-tomentose, bluish greenish, 11–13 cm. long, 5.5–9 cm. broad; seeds 2–2.3 x 1.2–1.4 x 0.9 cm.; fruiting peduncle robust, 7–8 cm. long, 1–1.5 cm. thick; germination epigeous.

According to Baker and his associates the cotyledons are white and the pulp is pale orange and of a very sweet taste.

The type collection of *T. calodesmis* was destroyed during the war in Berlin; it was collected by Hertha Schultze-Rhonhof near Papayacu at about 200 m. altitude on the Bonanza River, a tributary of the Pastaza River in eastern Ecuador. The description given by Diels makes it possible to identify his species perfectly with several Amazonian collections from nearby regions of Colombia, Peru, and Brazil. The sterile type specimen of *Theobroma glaucum*, collected on the Llanos de San Martín, agrees perfectly with a specimen that is almost a topotype, collected by Philipson, Idrobo, and Fernández in the foothills of the Sierra Macarena, Intendencia del Meta. I have no doubt that all these collections represent the same species, which extends from the upper Orinocia to upper Amazon basin on both sides of the great river.

Diels did not see fruits but gave an accurate description of the foliage and flowers; he related his species to *T. speciosum* on account of the texture and tomentum of the leaves, and also to *T. bernouillii*, but he says that the leaves are broader, the inflorescences larger, the flowers larger, and the staminodes longer.

COMMON NAMES.—Cacao de monte, cacao silvestre, chucú (Rio Papayacu [*Schultze-Ronhof*]), “bicco” Río Apaporis).

USES.—According to Karsten, the seeds are used as cacao by the natives, being very similar to the true cacao. Schultze-Rhonhof gives the indigenous name “chucú” for the fruit which, according to her, is very much appreciated by the natives.

DISTRIBUTION.—This species grows in the upper Amazon basin (northwestern section) along the rivers Caquetá, Caguán, Putumayo, Vaupés, Guainía, Inírida, and Apaporis in Colombia and along the Colombian boundary with Ecuador, Peru, and in western Brazilian Amazonas; at the northern end of its range it enters the Orinoco basin into the Meta drainage in Colombia.

It grows in the humid rain forests from the lower level of the great rivers to an altitude of 450 m. in forested hills.

COLOMBIA: META: Villavicencio, Llanos de San Martín, *Karsten*, s.n. (WU, holotype) (photo F. M. 32205). Sierra Macarena, Caño Yerly, 450 m., dense, humid forest; unbranched tree 10 m. high, bunches of cauliflorous fruits green, 24 XI 1949, *Philipson, Idrobo, & Fernández* 1552 (BM, COL, US).

PUTUMAYO: Vicinity of Mocoa; tree 6–7 m., growing fully exposed in meadow, trunk 23 cm. thick at base, branched inflorescence (dead) borne on trunk and branches, pod broadly pentagonal with 5 very shallow furrows, 13 cm. long, 9 cm. diam., blue green in colour, fruit pedicel 8 cm. long, 1.5 cm. diam., with abscission ring 1.5 cm. from pod base, in colour pale green with fine white hairs, 17 III 1953, *Holliday & Cope* T/79 (COL, TRIN, US). Ibidem; sterile tree 15 m. in forest, undoubtedly similar to T/79, shoots from below jorquette, *Holliday & Cope* T/79A (COL, TRIN, US). Río Leguízamo, Laguna Primavera, 3 IV 1953; tall tree 15 m., obviously cauliflorous, *Holliday & Cope* T/94 (COL, TRIN, US). Río Leguízamo; tree 16 m., with old trunk inflorescences, no flowers or fruits, 5 IV 1953, *Holliday & Cope* T/96 (COL, TRIN, US).

CAQUETÁ: Río Caguán, Camp 4; branched tree 10 m., found in good flowering condition, flowers in large inflorescences on trunk, 27 IV 1953, *Holliday & Cope* T/118 (COL, TRIN, U, US). Ibidem; tree 15 m., branched, two immature pods, on sloping land near T/114, 26 IV 1953, *Holliday & Cope* T/115 (TRIN, US).

VAUPÉS: Río Guainía, near Victorino, river level; tree without flowers or fruit but with stipules; said by the local Indians to be a type of cacao with small smooth pods, native in the forest, 3 II 1952, *R. E. D. Baker* 37 (TRIN, US). Río Inírida, Santa Rosa, 300 m.; tree 15 m., trunk about 30 cm. in diameter, bark greenish, cortex light red, wood white, no terminal growing point, young shoots arising from below jorquette, cauliflorous, pod surface 10-ridged, also with transverse ridges, fruit pedicel about 4 cm. long with abscission layer 3 cm. from trunk, 25 I 1953, *Bartley & Holliday* T/69 (COL, TRIN, US). Left bank of Río Inírida, San Joaquín, 200 m. from river bank, 300 m. alt.; tree 10 m., trunk base 15–20 cm. in diameter, one dead cymose inflorescence seen, 28 I 1953, *Bartley & Holliday* T/70 (COL, TRIN, US). Río Inírida, Río Papunana; tree 10 m., trunk about 30 cm. in diam., bluish gray in appearance, bark red, wood white, three branches at each jorquette, dichotomous branch habit, inflorescences on upper part of trunk, 18 II 1953, *Bartley & Holliday* T/74 (COL, TRIN, U, US).

AMAZONAS: Río Apaporis, Jinogojé, river level; tree 40–50 ft., 8''–9'' diameter at base, jorquettes of 3 branches, subsequent growth from below, ultimate branches repeatedly bifurcating, flowers in large clusters, sepals, ligules, and staminodes dark crimson, 8 IX 1952, *Baker & Cope* 11 (COL, F, TRIN, US). Ibidem (boundary Amazonas-Vaupés) between Río Piraparaná and Río Popeyaca, 250 m., Caño Unguyá; tree 8 m., calyx red, petals white, purplish red at apex, "bicco," 3–11 XI 1952, *García-Barriga* 14380 (COL, US).

BRAZIL: AMAZONAS: Sao Paulo de Olivença, on elevated land; tree 10 m., 12 cm. [in diam.], "cacau azul," 18 V 1945, *Fróes* 20942 (NY). Cidade Fonte Boa ("introduzida pelos indios do Japurá"); tree 10–12 m., 12–15 cm. diam., "cacau azul," "cachu azul," 4 IV 1945, *Fróes* 20645 (K, USDA). B. constant, tree 10 m., "cacau azul," 9 V 1945, *Fróes* 20885 (NY). Macacacain, Rio Jutahi, Barreira Branca; tree 15–25 feet, small, main branches in whorls of 3, each bifid, 31 I 1875, *Traill* 62 (GH, K, P).

6. *Theobroma bernouillii* Pittier

FIGURES 2, 6, 7, 15, 16, 17, 19; MAP 4; PLATE 5

Theobroma bernouillii Pittier, Repert. Sp. Nov. Fedde 13:319. 1914.

Chevalier (1946) 26: 277; León (1960) 314.

Theobroma asclepiadiflorum Schery, Ann. Mo. Bot. Gard. 29:360. 1942.

Theobroma capilliferum Cuatr. Rev. Acad. Colomb. Cienc. 6:547, figs. 3a, 4a, pl. 34. 1946.

Types.—*Pittier* 4105, Panama. *Wedel* 1535, Panama (of *T. asclepiadiflorum*). *Cuatrecasas* 16160, Colombia, Pacific coast (of *T. capilliferum*).

Tree 15–20 m. high; stem up to 25 cm. in diameter, with grayish-brown, rugulose bark 5 mm. thick and yellowish-white wood; sympodial growth by lateral, subterminal, upright shoots; primary branches ternate, grayish brown or blackish brown, dichotomous, the oldest falling off, leaving the stem naked, the terminal stem leafy, terete, dark brown, minutely, subappressed tomentulose, when older puberulous or glabrate; stipules linear-oblong, attenuate at apex, acute, pubescent, about 8 mm. long, 2.5 mm. wide.

Leaves coriaceous, more or less rigid, entire; petiole thick, 4–12 mm. long, terete, densely and minutely tomentulose, transverse rimose when dry; blades rather asymmetrically ovate, ovate-oblong, or elliptic-oblong, obtusely cuneate-attenuate and mostly very asymmetrical at base, triplinerved, narrowed toward the apex, ending in a long, linear, acute tip, the margin entire or very slightly sinuate, slightly revolute, 13–30 cm. long, 5.5–18 cm. broad, including the acumen, this 1.5–6 cm. long, 2–4 mm. broad, green or pale brownish above when dry, shining, the main nerves filiform, prominent, the others reticulate, slightly prominulous, pale greenish ochraceous or ashy beneath, apparently glabrous but the tawny shining veins with very sparsely minute stellate hairs and the areolae covered with very appressed, white tomentum of smaller, microscopic, entangled stellate hairs, the midrib and 5–7 secondary nerves on each side very prominent, the basal pair acutely ascending, the others distally curved-ascending, decurrent and anastomosing near the margin, the transverse tertiary nerves thin but prominent, the minor veins prominulous, minutely reticulate.

Inflorescences on the main trunk usually many-flowered, borne on short, tuberculate, woody branches, the panicles abundant, 4–10 cm. long, spreading, bristly, the axes slender (0.4–1.5 mm. thick), rigid, striolate, stellate-tomentose in the upper third or rarely from the base, cymose-bifurcate, corymbiform, the branchlets rigid, erect at acute angle; peduncles (ultimate branchlets) capillary, tomentulose, 2–20 mm. long, 3-bracteolate at apex; bracteoles narrowly linear, 1–2 mm. long, very soon deciduous; pedicels thicker than the peduncles, about 5–20 mm. long at anthesis, minutely stellate-tomentellous like the branchlets; buds ovoid, densely and shortly tomentose.

Flowers crimson; sepals moderately thick, lanceolate-oblong, rather acute, shortly united at base, often first temporarily united in pairs but separated later, 8–10 mm. long, 3 mm. wide, reddish, with sparse slender, flexuous, sericeous hairs inside, ferruginous, rugulose, and

stellate-tomentose outside, minutely tomentulose at the margin inside, with thick, glandular hairs crowded at the insertion at base; petal-hood red, oblong-obovate, rounded-cucullate at apex, narrowed at base, 3-nerved, prominent inside, hirtellous pubescent outside, 4–5 mm. long, about 2 mm. wide, at base 0.6 mm. wide; petal-lamina crimson, sessile, shortly unguiculate-articulate, moderately thick, rugulose, glabrous, orbicular or suborbicular or elliptic, minutely crenulate, 2.5–4 mm. long, 3–4 mm. broad; staminal tube about 1.5–2 mm. high; staminodes 6–9 mm. long, erect in bud, purplish red, sublanceolate-linear-subulate, thick, suddenly narrowed toward the apex, covered with minute, spreading, acute, conical trichomes; fertile filaments glabrous, flexuous, about 2.5 mm. long, 2-antheriferous; ovary 5-sulcate-costate, tomentose, 1.2 mm. high; styles five, 2 mm. long, adherent into a column but separable.

Fruit 15–20 (12–25) cm. long, 6–7.5 (5.2–8) cm. broad, ellipsoid-oblong, more or less prismatic, obtusely 5-angulate, abruptly narrowed subacute or subobtuse at apex, umbilicate at base, more or less constricted near the base or not; pericarp thick, rigid, coriaceous at maturity, the epicarp and endocarp hard coriaceous, the mesocarp fleshy, shrinking in drying, dull brown, dense velvety-tomentose; seeds compressed-ovoid, 16–22 x 9–14 x 9–11 mm., the testa reddish, papery, the cotyledons white; pulp white, flavored, acidulous; germination epigeous.

This species, as here broadly considered, includes heteromorphic elements described as three species, two of which came from the Atlantic coast of Panamá, and the third from the Pacific coastal region of Colombia. The Colombian population (*T. capilliferum*) is the best known, being represented by several collections with fruits and flowers, showing morphological uniformity throughout its area. The original *T. bernouillii* is known only from flowering material of one collection (the type), which has some minor differences from the Colombian plants in the shape of the leaves and details of flowers. The other described Panamanian species, *T. asclepiadiflorum*, was based on discordant elements collected by von Wedel in Water Valley. Schery wrote: "Although fruiting material of this species is lacking, floral and vegetative characters distinguish it sufficiently to warrant description as a new species." The glabrous branches and leaves of the type specimen, which resemble those of *T. cacao*, do not belong to a *Theobroma*; they belong actually to the Lauraceae. The inflorescences and flowers are similar to those of *T. bernouillii*, type specimens of which were collected by Pittier not very far away. The question about what kind of leaves belong to the described flowers of *T. asclepiadiflorum* is answered by the collection Wedel 681 from the same locality, Water Valley; the flowers of this collec-

tion are identical to those of the type of *T. asclepiadiflorum* and the leaves are exactly like those of *T. bernouillii*. There are minor differences between the flowers of these two types, but considering the vicinity of the geographic range of these two populations, it may be safe to consider them mere forms of one species. Fruits from the type locality of *T. bernouillii* have never been collected, but Allan Lucas did collect fruits of *T. asclepiadiflorum* in Water Valley. The flowers of *T. asclepiadiflorum* are almost identical to those of *T. capilliferum*, but the fruits are smoother and not constricted.

In view of these facts, I consider all these Colombian and Panamanian plants to belong to one species; since the three forms are geographically separated the observed differences warrant subspecific recognition.

DISTRIBUTION: Pacific coast and the Chocó region of Colombia and the Atlantic coast of Panama. In the underforest of the tropical rain forest, from sea level and lowland swamps to heavily forested hills about 100 m. altitude.

Key to Subspecies of *Theobroma bernouillii*

1. Leaves broadly ovate or ovate-oblong, very asymmetrical, rigid, 5–12 x 2–6 cm. Petal-lamina orbicular 2.5–3.5 mm. long; petal-hood 4–5 x 2 mm.; staminodes subulate, densely pilosulous, 7–8.5 mm. long; inflorescences long, with thin branches, the peduncles 5–20 mm. long, the pedicels about 10 (5–20) mm. long; fruits obtusely pentagonal with smooth, conspicuous ridges, 12–25 x 5–8 cm., umbilicate constricted above the base.

6c. subsp. **capilliferum**

1. Leaves oblong-elliptic, slightly asymmetrical, thinner, less rigid.
2. Staminodes lanceolate, slightly pilose, 5.5–6 mm. long, 1.5–2 mm. broad at base; petal-lamina suborbicular, 3 x 3–4 mm. long; petal-hood 4–5 x 2–2.5 mm.; peduncles 2–5 mm. long; pedicels 5–8 mm. long; fruit unknown.

6a. subsp. **bernouillii**

2. Staminodes subulate, densely pilose, 9–10 mm. long, 1.5 mm. broad; petal-lamina elliptic, 4 x 3 mm.; petal-hood 5 x 3 mm.; peduncles 6–12 mm. long; pedicels 10–12 mm. long; fruit oblong, 17 x 7 cm., very slightly pentagonal, attenuate at apex, not contracted at base, with a filiform, impressed, furrow on each inconspicuous ridge.

6b. subsp. **asclepiadiflorum**

6a. *Theobroma bernouillii* Pittier subsp. **bernouillii**

DISTRIBUTION.—Atlantic coast of Panama.

PANAMA: Prov. Colón, in forests near Fató, Loma de la Gloria (Nombre de Dios), 10–104 m., 4 VIII 1911, *Pittier* 4105 (US holotype; isotypes BM, BR, C, F, GH, K) (Photo USNH 3199).

Further collections at the type locality are necessary to know the nature of the fruits.

6b. *Theobroma bernouillii* Pittier subsp. *asclepiadiflorum* (Schery) Cuatr., stat. nov.

Theobroma asclepiadiflorum Schery, Ann. Mo. Bot. Gard. **29**:360. 1942; León (1960) 316, 321, fig. (as. *T. bernouillii*).

TYPE.—*Wedel* 1535, second sheet, flowers (MO, lectotype).

DISTRIBUTION.—Atlantic coast of Panama.

PANAMA: Bocas del Toro: Water Valley, vicinity of Chiriquí Lagoon; tree 90 feet, flowers red, 8 XI 1940, *H. von Wedel* 1535 (second sheet MO, lectotype); the first sheet of this collection (MO) belongs to the Lauraceae. Bocas del Toro, Water Valley, 10 IX 1940; tree 80 ft.; flowers maroon red, *H. von Wedel* 681 (MO). Bocas del Toro, Water Valley, V 1949, *Allan Lucas* 1 (F, TURRI).

The fruit of this subspecies is known through one specimen brought by Allan Lucas (TURRI), which is 17 x 7 cm., ellipsoid-oblong, very slightly pentagonal with 5 filiform furrows on the obtuse angles; the surface is slightly rugose due to the drying; the apex is shortly attenuate and the base is subtruncate and umbilicate. The shape differs clearly from that of the fruits of subsp. *capilliferum* and *T. glaucum*; it must be a mutant form geographically isolated.

6c. *Theobroma bernouillii* Pittier subsp. *capilliferum* (Cuatr.) Cuatr., stat. nov.

PLATE 5

Theobroma capilliferum Cuatr. Rev. Acad. Colomb. Cienc. **6**:547, figs. 3a, 4a, pl. 34. 1946; Baker, Cope & al. (1954) 13, figs. 17, 18; León (1960) 314, 317, fig.

TYPE.—*Cuatrecasas* 16160, Colombia, Pacific coast.

COMMON NAMES.—Chocolate de monte, cacao de monte bravo, cacao de monte (Colombia).

USES.—On the Pacific coast of Colombia and in the Chocó area, the fruits are known as wild cacao (chocolate de monte, cacao de monte, cacao de monte bravo). Their white seeds are considered a high quality cacao, but the fruits remain abandoned on the trees, the people not making actual use of them, although monkeys and other animals break or pierce them, sucking the pulp or eating the seeds.

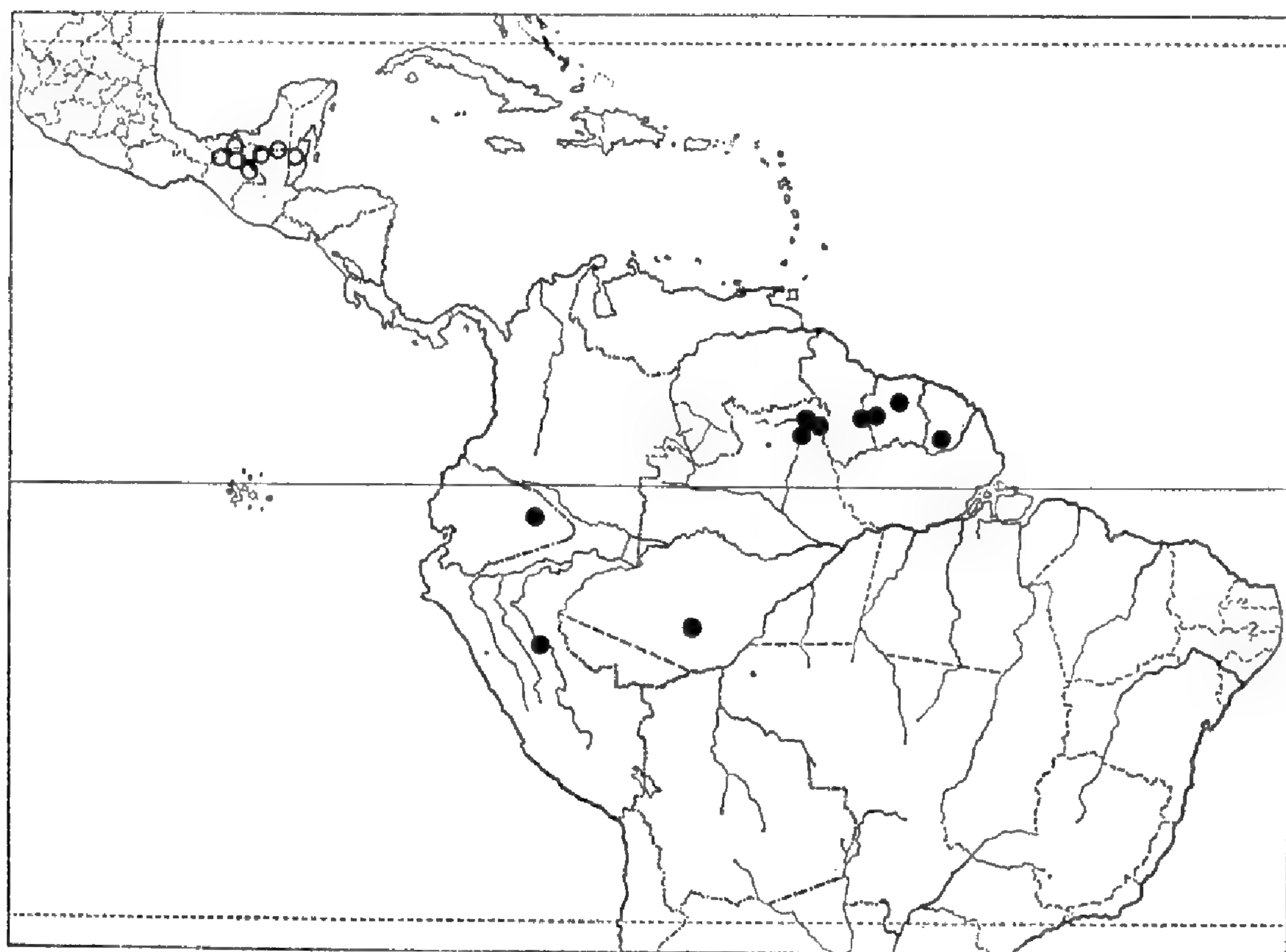
DISTRIBUTION.—Pacific Coast and the Chocó region of Colombia. In the under story of the rain forest, from the lowland swamps next to the mangroves to the forested hills about 100 m. in altitude.

COLOMBIA: EL VALLE: Pacific Coast, Río Yurumanguí, Veneral, swampy rain forest in Quebrada del Zancudo, 5 m. elevation; tree 15 m., 25 cm. diam. at base, bark granulate-rugose, brown or grayish, its section 5 mm. thick, producing abundant mucilage; wood yellowish white; fruits 11–12 x 6 cm. (immature), ellipsoid-prismatic, thick, umbilicate at base, more or less constricted above the base, with 5 furrows or flat sides, and 5 well-marked angles, apex acute and slightly umbilicate, the surface minutely tomentose, greenish ferruginous, peduncles 6–10 cm. long, thick, fruits abundant, hanging on trunk, leaves coriaceous, rigid, green above, pale green beneath, long-tailed (Cuatr. photographs C-2202, 2203), 10 II 1944, *Cuatrecasas* 16160 (VALLE, holotype; isotype, F). Pacific

Coast, Río Cajambre, Barco, forest on hill at the right margin of Quebrada de Agua Clara, 40–100 m. elevation; tree 20 m., stem 25 cm. diam., leaves coriaceous, pale yellowish green above, cinereous beneath, distichous and pendulous, the lower ones larger and thicker, dry inflorescences with thin, long branchlets, fruiting peduncles 8–10 cm. long, 10–12 mm. thick, fruits with 5 furrows and 5 thick angles, surface sinuate-rugose, velvety-tomentose, pale tawny, 16–20 cm. long, 6.5–7.5 cm. broad, umbilicate at both ends, usually constricted above the base, cotyledons whitish, wood yellowish white, 23 IV 1944, *Cuatrecasas* 17034 (F, VALLE). Same locality and date, seedlings, *Cuatrecasas* 17034A (F, VALLE). Río Cajambre, San Isidro, hill forest on left margin of Quebrada de Veneno, about 50 m. alt.; tree 20 m., stem 20 cm. diam., bark yellowish white, leaves coriaceous, rigid, yellowish green above, greenish cinereous beneath, fruits hanging on trunk, 4 V 1944, *Cuatrecasas* 17350 (F, VALLE). Same locality, seedlings, *Cuatrecasas* 17350A (F, VALLE). Río Calima, Caño de la Brea, about 5–10 m. elev.; tree 15–20 m. high, 20–25 cm. diam. at base, crimson flowers in dense cushions on upper portion of trunk only, 29 VI 1943, *Holliday* T/142 (TRIN, US). Río Calima, Estación Agroforestal, about 5–10 m. alt.; tree 12–15 m. in forest clearing, crimson flowers in dense cushions on upper part of trunk only, dry fruit up to 25 x 8 cm., ridged, 29 VI 53, *Holliday* T/145 (TRIN, US).

CHOCÓ: Lloró, young tree, sterile, 4 VIII 1953, *Holliday & Bartley* T/177 (TRIN, US). Ibidem; tree 6 m., *Holliday & Bartley* T/178 (TRIN, US). Río San Juan, Remolino, young tree 2 m., sterile, 1 VIII 53, *Holliday & Bartley* T/172 (TRIN, US).

NARIÑO: South of Tumaco, in heavy rain forest; tree 10 m., fruits on trunk, olivaceous, 18 X 1955, *Romero Castañeda* 5405 (COL).



MAP 6.—Location of known spontaneous, wild, populations of *Theobroma cacao* subsp. *cacao* ○ and subsp. *sphaerocarpum* ● which may be the origin of the present cultivated varieties.

Section 3. *Theobroma**Theobroma* sect. *Theobroma*

FIGURES 3, 4

Theobroma sect. *Cacao* (Aubl.) Bernoulli, Uebers. Art. *Theobroma* 4. 1869.Sect. *Eutheobroma* subsect. *Cacao* (Aubl.) Pittier, Rev. Bot. Appl. 10 (110):779. 1930.

Petal-laminas spatulate, long-attenuate stipitate. Petal-hoods 3-nerved. Staminodes linear-subulate, erect in aestivation. Filaments 2-antheriferous. Fruit ovoid-oblong or ellipsoid, more or less pentagonal, the pericarp thick, firmly fleshy glabrous. Cotyledons epigeous at germination. Leaves glabrous or sparsely pilose. Inflorescences on the trunk and on leafy branches. Sympodial growth of stem by orthotropic adventitious, lateral-subterminal shoots. Primary branches in 5's, persisting in age.

TYPE SPECIES.—*Theobroma cacao* L.

7. *Theobroma cacao* L.

- FIGURES 1, 2, 3, 5, 6, 20, 21, 22, 23, 24, 25, 26; MAP 6; PLATE 6
- Theobroma cacao* L. Sp. Pl. 2:782. 1753; Syst. Nat. ed. 12, 2:508. 1767; H. B. K. (1823) 316; Richard (1845) 183 (1845a) 73; Bernoulli (1869) 5, pl. 1, 2; Baillon (1884) 792–795, figs.; Schumann in Mart. (1886) 72, pl. 7; Jumelle (1899) 11, figs. 1–9; Preuss (1901), pls. 1, 2; De Wildeman (1902) 91, figs. 16, 18, 20, 21. 1902; Standley (1923) 805; Ducke (1925) 130; (1940) 268, pl. 1, fig. 1, (1954) 11; Fawcett & Rendle (1926) 158–160, fig. 60; Uittien in Pulle, Fl. Surinam 3:45. 1932; Ciferri (1933) 604; Standley (1937) 688; Chevalier (1946) 269–274, pl. 5; Standley & Stey. (1949) 423; Holdridge (1950) 4; Addison & Tavares (1951) 25, pl. 7, pl. 13, fig. 7; Lemée (1952) 379; Baker, Cope & al. (1954) 9–11; Cuatrecasas (1956) 653; León (1960) 311–313.
- Cacao* Clusius, Exot. Libr. Dec. 55. 1605; Ray (1688) 1670; Sloane (1696) 134; Tournef. (1700) 660, pl. 444; 1700; Merian (1705), pl. 26; Sloane (1725) 15, pl. 160; Ray (1733) 158; Weinm. (1739) 1–11, pl. 277, 278; Geoffr. (1747) 409; Catesb. (1747) 6, pl. 6; Blackwell (1739) 373; Hernández (1630) 79, (1946) 908–914.
- Amygdalis similis guatimalensis*, *Avellana mexicana* Bauh. Pinax Theat. Bot. 442. 1623.
- Arbor cacavifera americana* Pluk. Almagest. Bot. 40, pl. 268. 1696.
- Theobroma foliis integerrimis* Linn. Hortus Cliff. 379. 1737.
- Cacao guianensis* Aubl., Pl. Guian. 2:683, pl. 275, figs. 1–15. 1775, pro parte (*tantum flores*).
- Cacao sativa* Aubl., Pl. Guian. 2:689. 1775; Lam. Encycl. Meth. 1:533, pl. 635. 1797.
- Cacao minus* Gaertn. Fruct. & Sem. 190, pl. 122. 1791.
- Cacao Theobroma* de Tussac. Fl. Antill. 1:101, pl. 13. 1808.
- Theobroma integerrima* Stokes, Bot. Med. 4:83. 1812.
- Theobroma caribaea* Sweet. Hort. Britt. 67. 1830 (nom. nud.)
- Theobroma pentagona* Bernoulli, Uebers. Art. *Theobroma* 6–7, pl. 2. 1869; Preuss (1901) 199, 255, pl. 3, 5; De Wildeman (1902) 94; Standley & Stey. (1949) 427.
- Theobroma leiocarpa* Bernoulli, op cit. 6, pl. 2; Standley (1937) 688; Standley & Stey. (1949) 426.

Theobroma Saltzmanniana Bernoulli, *op. cit.* 7, *pl.* 2.

Theobroma Kalagua De Wild., Bull. Herb. Boiss. 7:957, *pl.* 11. 1899 (*tantum folia*, sed lectotypus).

Theobroma sativa (Aubl.) Lign. et Le Bey, Bull. Soc. Linn. Norm. V, 8:263. 1904; Chevalier (1946) 270.

Theobroma sphaerocarpa Chevalier, Veget. Util. Afr. Trop. Fr. 4:12. 1908.

Theobroma sapidum Pittier, Bol. Soc. Venez. Cienc. Nat. 1:183. 1932, *nom. nud.*

Theobroma cacao var. *typica* Ciferri, Monogr. 604. 1933.

Theobroma cacao var. *leiocarpa* (Bernoulli) Ciferri, Monogr. 604. 1933.

Theobroma cacao var. *typica* x *T. cacao* var. *leiocarpa*, Ciferri, 604. 1933.

Theobroma cacao forma *leiocarpum* (Bernoulli) Ducke, Rodriguesia 4:274. 1940.

Theobroma sativa var. *leucosperma* Chevalier, Bull. Inter. Bot. Appliq. 26:270. 1946.

Theobroma sativa var. *melanosperma* Chevalier, *loc. cit.*

Theobroma cacao subsp. *leiocarpum* (Bernoulli) Cuatr. in Macbr. Fl. Peru, Field Mus. Publ. Bot. 13 (3A):654. 1956.

Theobroma cacao subsp. *sativa* (as (Lam.) Lign. & Le Bey) León in Hardy's Cacao Man. 312. 1960.

Theobroma cacao subsp. *pentagona* (Bernoulli) León, *loc. cit.*

TYPE.—Sloane Herbarium vol. 5, p. 59 (BM, lectotype); Paratype: Tournefort *pl.* 444, fruit-lectotype.

Tree usually 4–8 m. high, rarely taller (up to 20m.), with the growth of the sympodial stem by subterminal, lateral, upright shoots (chupons); primary branching by successive whorls of normally spreading branches; young branchlets terete, grayish green or brownish, densely or sparsely pubescent, with slender, patulous, acute, simple or furcate hairs 0.1–0.3 mm. long, later glabrate, more or less striate, rugulose and sparsely lenticellate; stipules subulate, very acute, 5–14 mm. long, 0.5–1.5 mm. wide at base, pubescent or puberulous, deciduous.

Leaves coriaceous or chartaceous, more or less rigid, alternate, distichous on the normal branches, green; petioles pubescent or tomentose, with simple, acute, slender, rather dense, spreading hairs, thickened pulvinate at the ends, 1.5–2 (1–3) cm. long, on orthotropus stems 3–10 cm. long; blades subobovate-oblong or elliptic-oblong, slightly asymmetrical, rounded or obtuse at base, attenuate and cuspidate at apex, acute or subacute, usually entire or slightly and irregularly sinuate, green above, pale when dry, glabrous except for the pubescent or puberulous midrib, the midrib linear, prominent, the secondary nerves filiform, the fine veins reticulate, often slightly prominent, lighter green beneath, glabrous or with very sparse, minute, simple, furcate or stellate hairs, rarely puberulous, the midrib thick and prominent, the secondary nerves 9–12 each side, prominent, subpatulous, then ascending, near the margin curving, slendering, anastomosing, the tertiary nerves prominent, the minor veins reticulate and prominulous, 15–50 cm. long, 4–15 cm. broad, the acumen 1–2.5 cm. long.

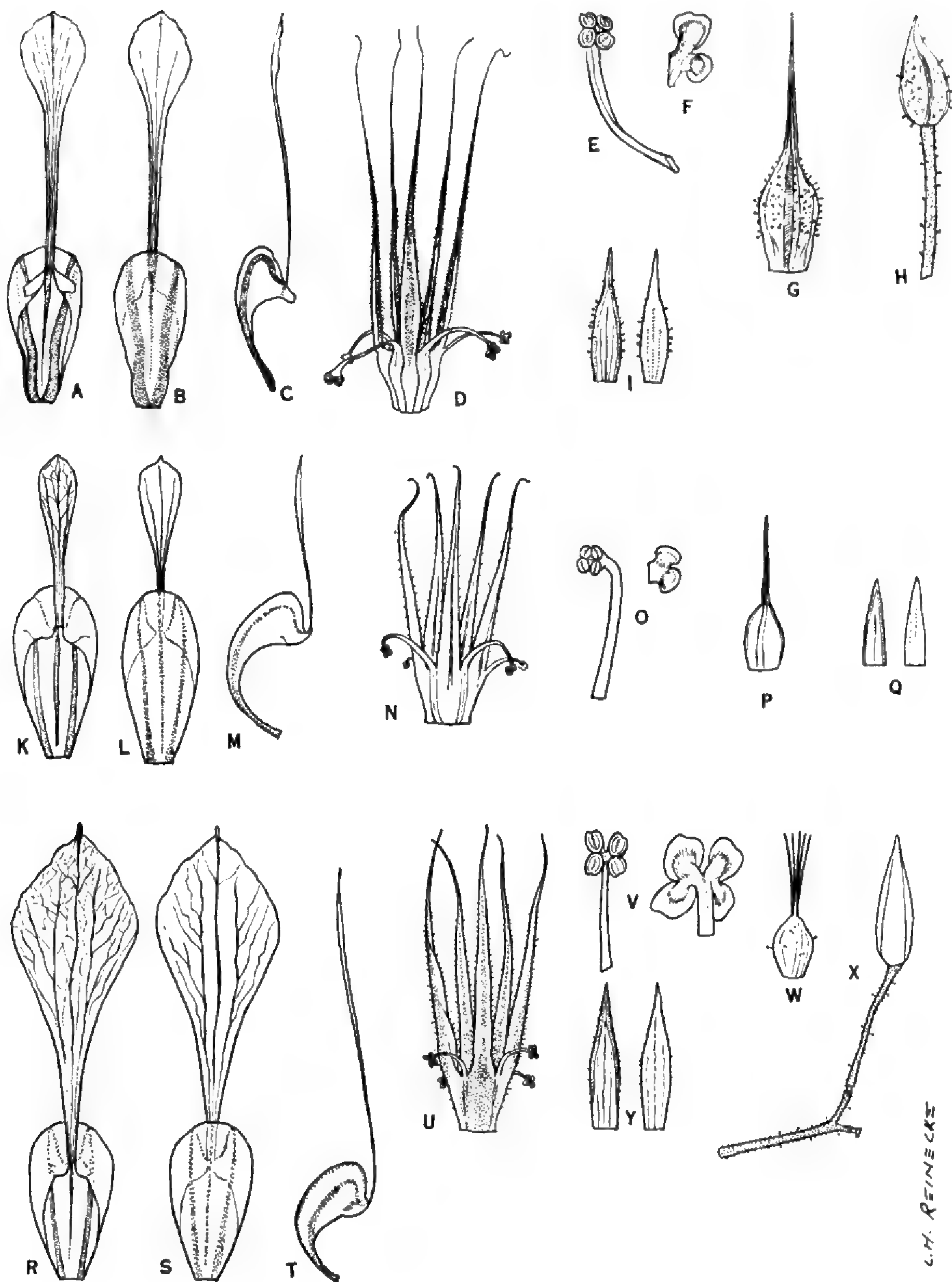


FIGURE 20.—A-I, *Theobroma cacao* subsp. *cacao* fma. *pentagonum* (Cuatr. 26004): A, B, C, petal from inside, outside and laterally, $\times 5$; D, androecium, $\times 5$; E, stamen, $\times 10$; F, anther, $\times 20$; G, pistil, $\times 10$; H, bud, $\times 2$; I, sepal from inside and outside, $\times 2$. K-Q, *T. cacao* subsp. *sphaerocarpum* (Cuatr. 7756): K, L, M, petal from inside, outside and laterally, $\times 5$; N, androecium, $\times 5$; O, stamen, $\times 10$ and anther, $\times 20$; P, pistil, $\times 5$; Q, sepal from inside and outside, $\times 2$. R-Y, *T. cacao* subsp. *cacao* (Nelson 2490): R, S, T, petal from inside, outside and laterally, $\times 5$; androecium, $\times 5$; V, stamen, $\times 10$ and anther, $\times 20$; W, pistil, $\times 5$; bud and pedicel, $\times 2$; Y, sepal from inside and outside, $\times 2$.

L.H. REINECKE

Inflorescences on the trunk and branches, usually borne on small tubercles, the cymose branchlets short, knotty, persistent, the cymose peduncles 1–3 mm. long, stellate-pubescent, hirtellous and with scattered glandular trichomes; bracts ovate or ovate-oblong, amplexant, pubescent; bracteoles ovate-oblong, acute or subacute, 0.5–1.2 mm. long, pubescent, deciduous; pedicels capillary, rigid, pale green, whitish or reddish, 5–15 mm. long, hirtellous with rather dense, thin,

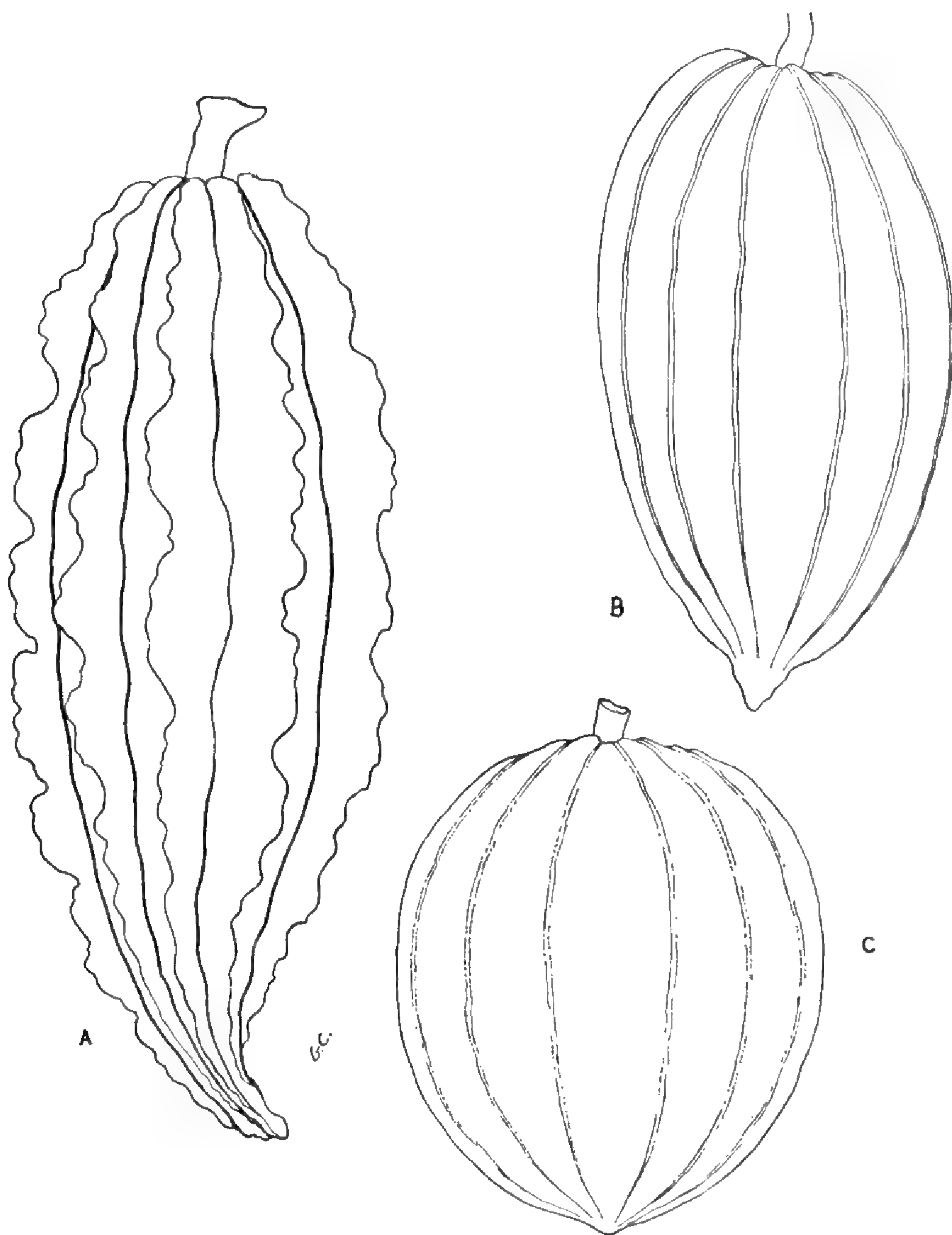


FIGURE 21.—Sketches of fruits of *Theobroma cacao* from classical and recent literature: A, in Tournefort plate 444, clearly representing a “criollo type”; B, in Sloane, pl. 160; C, in Chevalier 1946, pl. 5 (*T. sphaerocarpum* Chev.).

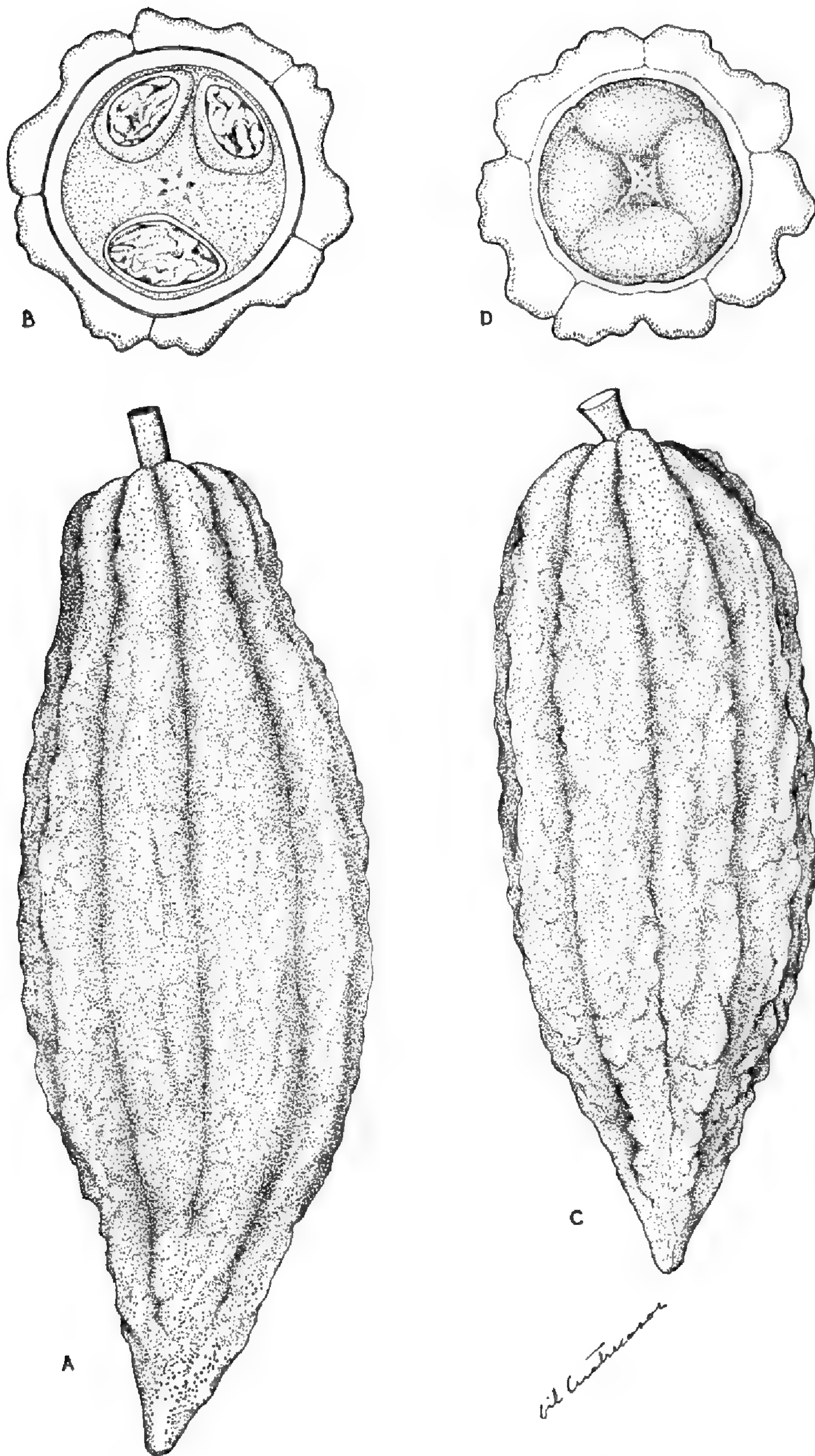


FIGURE 22.—A, Fruit of *Theobroma cacao*, cultivar “cundiamor” (Cuatr. 26492 from Colombia). B, Cross section of same showing structure of pericarp and arrangement of seeds each surrounded by their pulp. C, *T. cacao* subsp. *cacao*, cultivar “criollo” (“Caldas”) (Cuatr. 26006 from Colombia). D, Section of same. All $\times \frac{1}{2}$.

acute, patulous, stellate or furcate hairs and sparse pluricellular, glandular, capitate trichomes; buds white, whitish green, lilac, or reddish, ovoid or oblong-ovoid, acute, 5–7 mm. long, subglabrous or sparsely puberulous with slender stellate hairs and thicker, glandular,

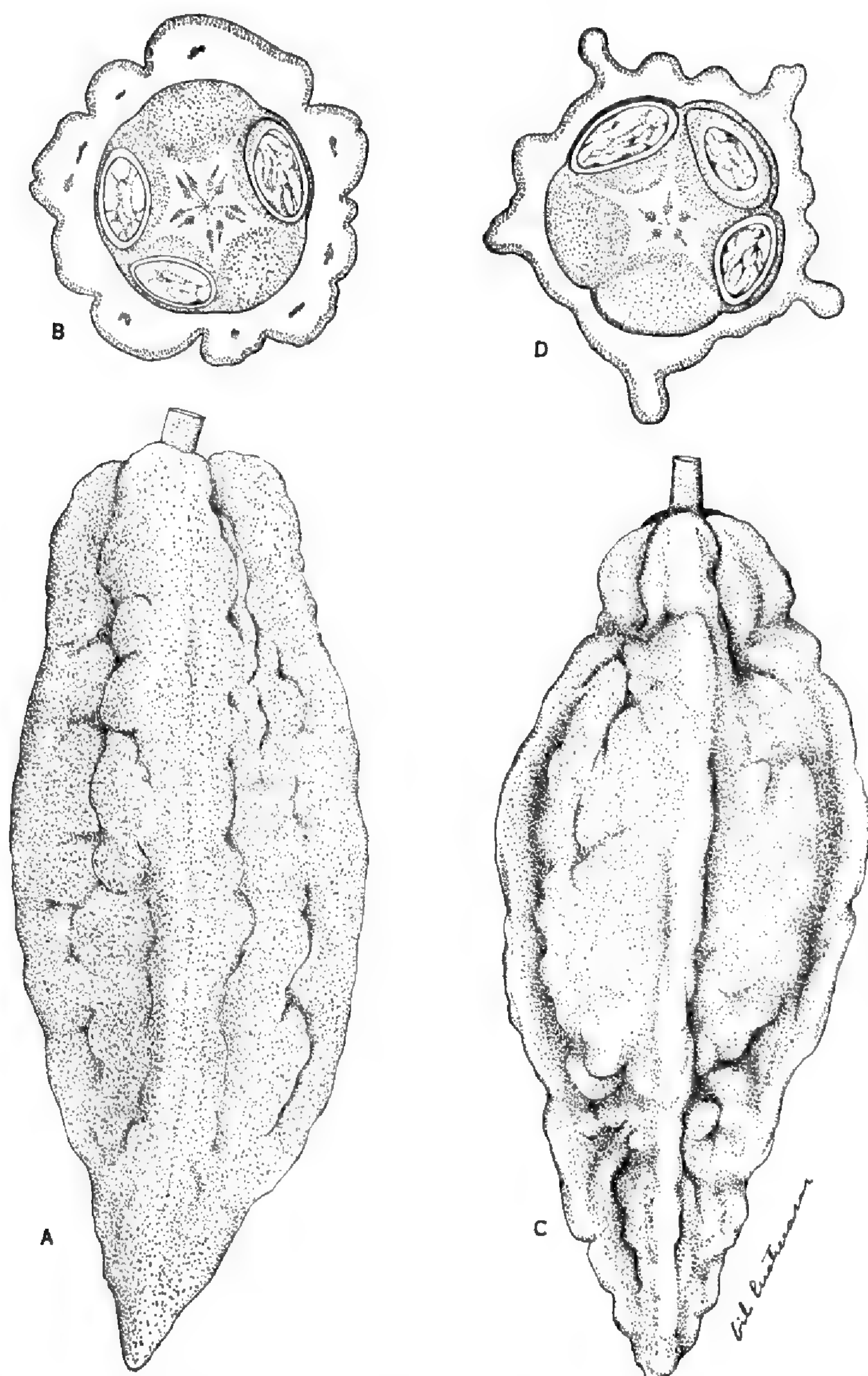


FIGURE 23.—A, Fruit of *Theobroma cacao* subsp. *cacao* fma. *pentagonum* (Cuatr. 26004 from Colombia) with some degree of introgression from fma. *cacao*. B, transection of the same showing the great reduction of the structure of pericarp (mesocarp represented by isolated bundles). C, *T. cacao* subsp. *cacao* fma. *pentagonum*, typical (Cuatr. 26540 from Costa Rica). D, transection of the same, showing the pericarp reduced to one layer. All $\times \frac{1}{2}$. Cultivar "lagarto."

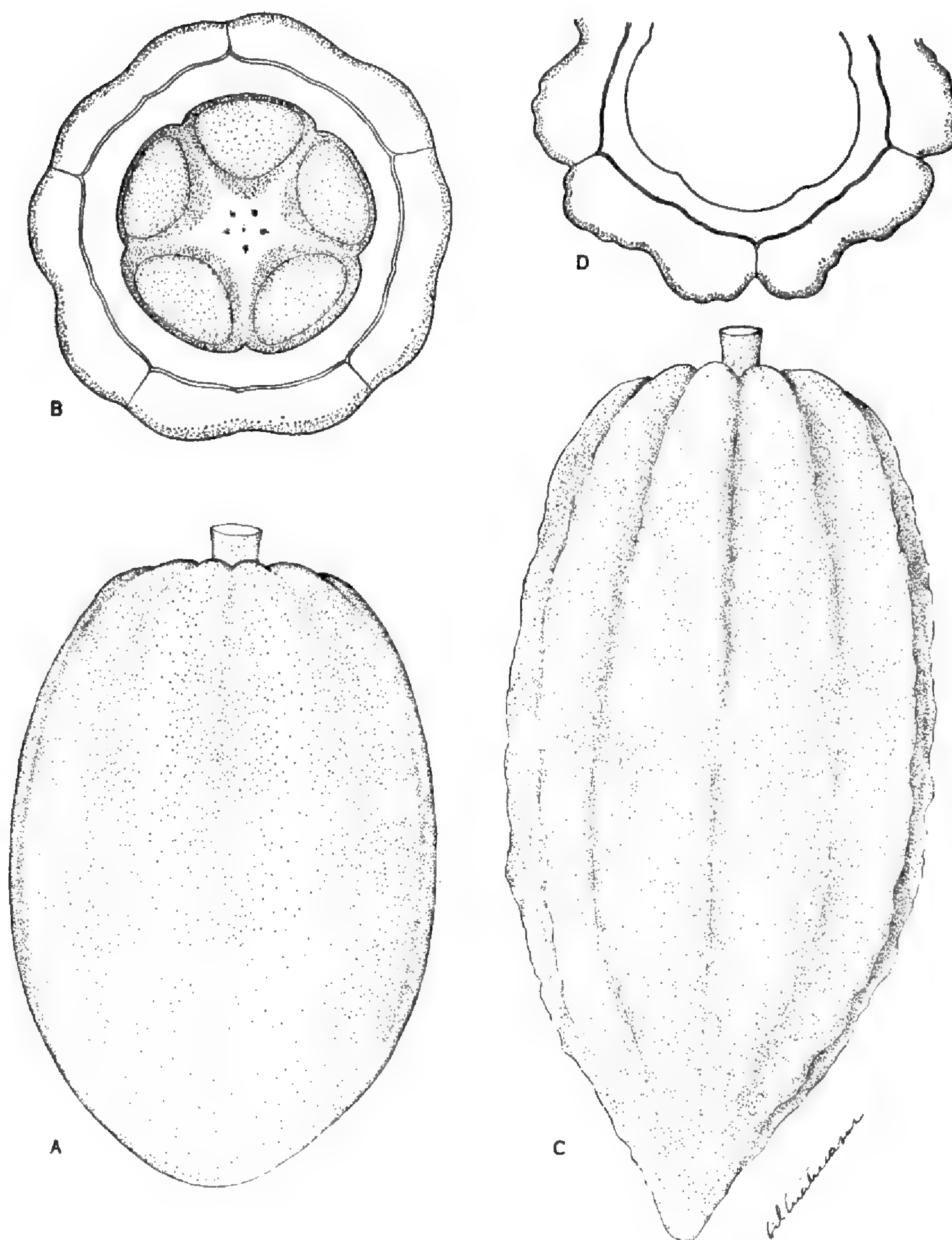


FIGURE 24.—A, Fruit of *Theobroma cacao* subsp. *sphaerocarpum*, cultivar “amelonado” (Cuatr. 25805 from Venezuela, Barlovento). B, transection of the same. C, fruit of *T. cacao* cultivar “angoleta” (Cuatr. 26494 from Colombia). D, transection of same. All $\times \frac{1}{2}$.

stipitate trichomes; sepals thick-membranaceous, lanceolate or oblong-lanceolate, acute, white, greenish white, pale violaceous or reddish, slightly 3-nerved, shortly (0.5–1 mm.) united at base, 5–8 mm. long, 1.5–2 mm. wide, minutely tomentose at margin, outside sparsely pubescent with stellate and glandulose hairs, or glabrous, inside glabrous or with rare glandular trichomes; petals contorted in aestivation, thick-membranaceous, the hood 3–4 mm. long, 5–2 mm. wide,

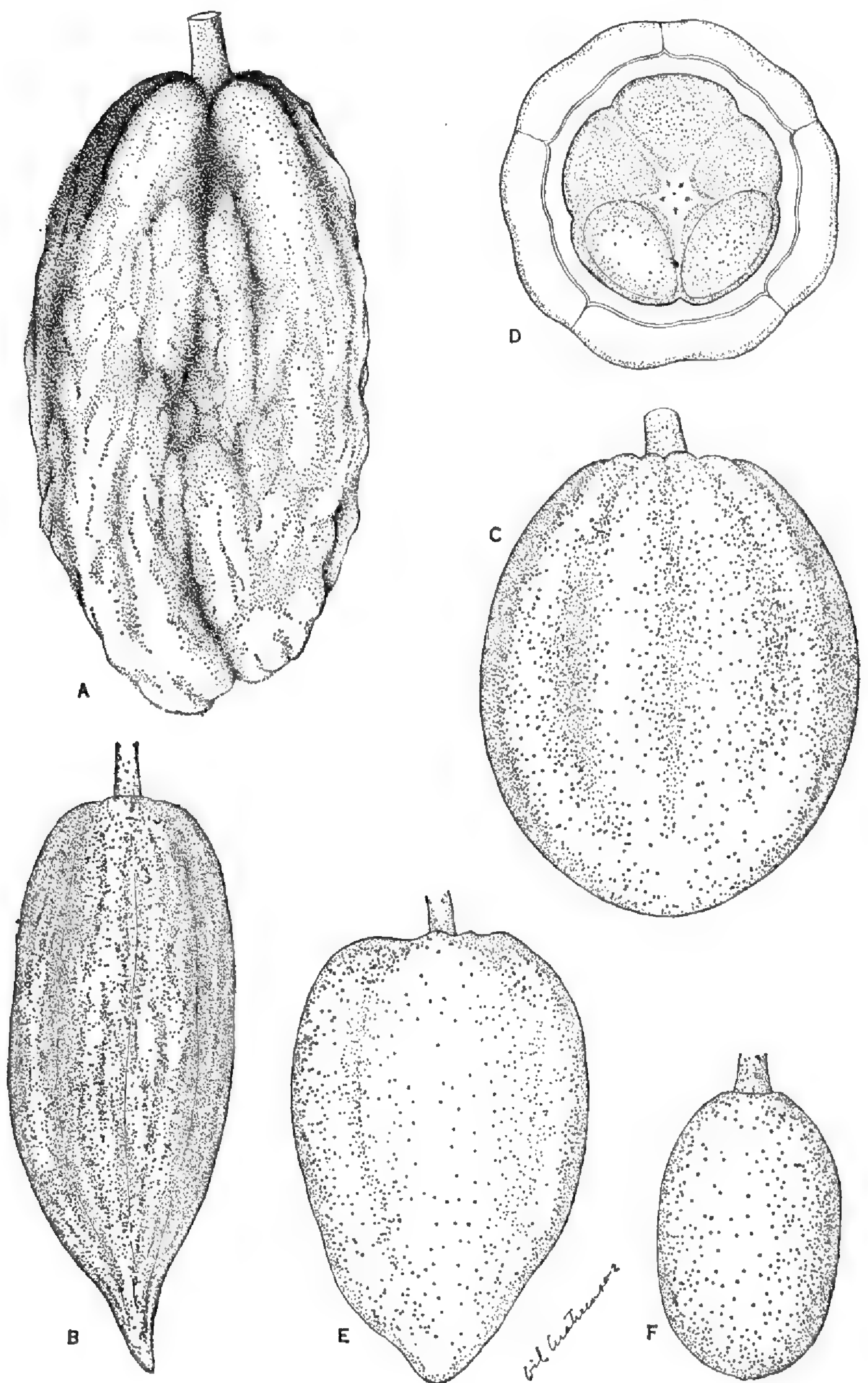


FIGURE 25.—A, Fruit of *Theobroma angustifolium* (Cuatr. 25790). B, fruit of *T. cacao* subsp. *cacao* fma. *lacandonense* (Miranda 9299). C, *T. cacao* subsp. *sphaerocarpum* cultivar “calabacillo” (Cuatr. 25805P from Venezuela). D, section of the same. E, fruit of *T. cacao* subsp. *cacao* f. *leiocarpum* from the original drawing by Bernoulli. F, *T. hylaeum* (Araque & Barkley 18C745). All $\times \frac{1}{2}$.

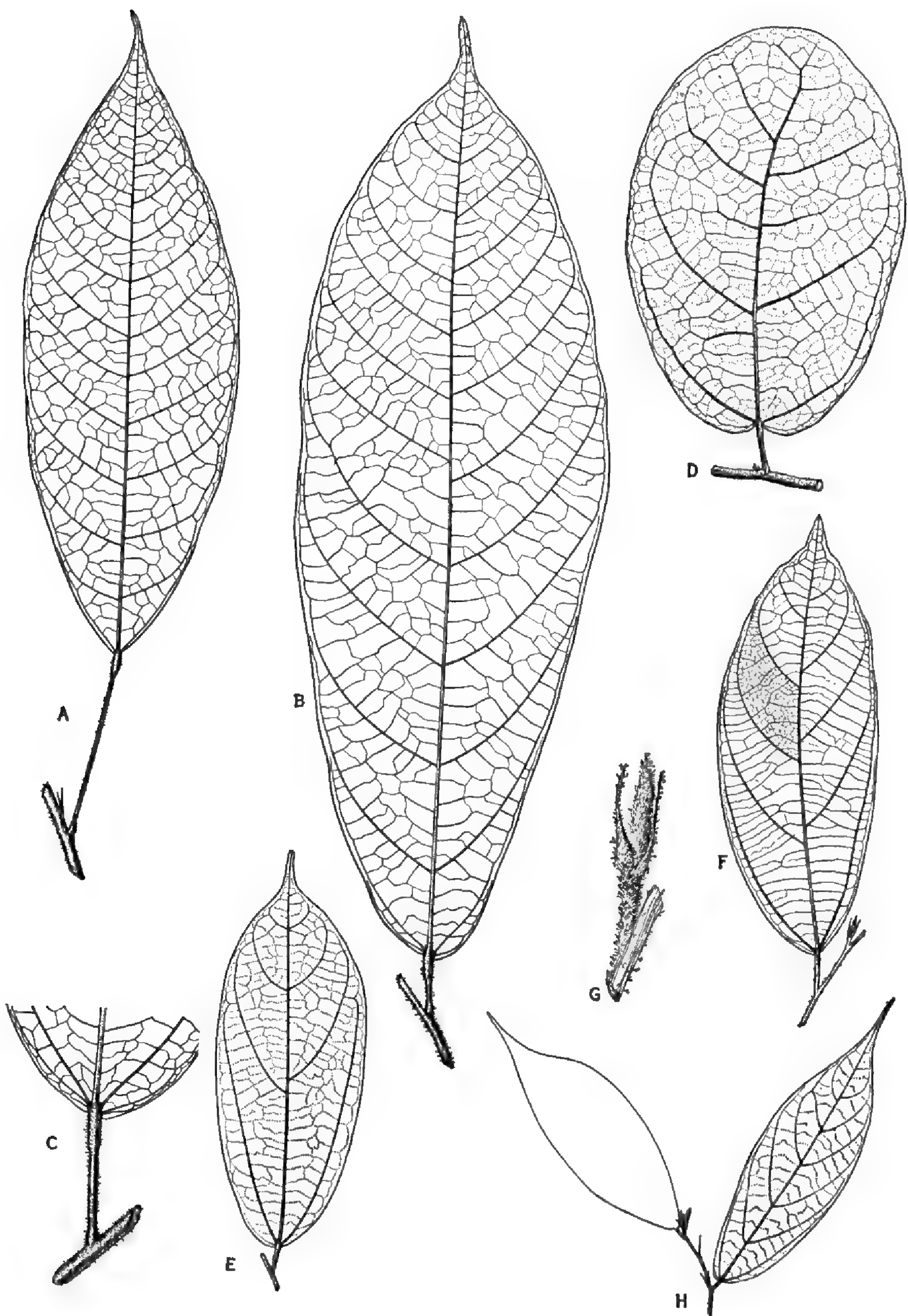


FIGURE 26.—A-C, Showing the characteristic elongated, bipulvinate petiole in *Theobroma cacao*: A, *T. cacao* from orthotropic stem (Steyermark 54143); B, *T. cacao* from lateral branches (Cuatr. 7756); C, *T. cacao* from young, lateral branches (Steyermark 49218). D, exceptional, broad, rounded leaf of *T. cacao*, a cultural mutation (León 5078). E, F, *T. microcarpum* (Fröes 23963 and Holliday & Cope 125). G, young shoot showing pubescence and stipules of *T. microcarpum* (Holliday & Cope 125). H, *T. gileri* (Giler 162). G, $\times 3$; leaves, $\times \frac{1}{2}$.

obovate, rounded at apex, white, 3-nerved, the nerves papillose inside, the lateral ones very thick, usually purplish or red, the medial prominent only upwardly; petal-lamina pale yellowish, 1.5–2.5 mm. long, 1.5–2 mm. wide, obovate or rhombic-obovate, attenuate at apex, acuminate or subtruncate and shortly mucronate, rarely blunt, entire or sinuate at margin, pedicellate at base, the pedicel linear, 3-nerved and sometimes 4- or 5-nerved at apex, 2–4 mm. long, 0.2–0.5 mm. wide; androecium tube rather thick, 1.2–1.5 mm. long, glabrous; staminodes 4–6 mm. long, 0.6–0.7 mm. broad at base, narrowly subulate, very acute, erect in bud, erect or somewhat flexuous in anthesis, the middle vein thick, angular, red or purplish, minutely papillose-pilose, the thin margin whitish, more or less revolute, ciliate, with slender, flexuose simple hairs; stamens diantheriferous, the filaments glabrous, patulous or recurved, 1.5–2 mm. long, the anthers about 0.4 mm., with rounded cells; ovary oblong-ovoid, obtusely pentagonal or 5-ridged, about 1.5 mm. high, 0.8 mm. thick, glabrous or usually glandular, covered with more or less copious white or reddish, pluricellular, stipitate glands; styles 5, glabrous, adherent, 1.5–2.5 mm. long.

Fruit subbaccate, variable in shape, from globose to fusiform and acute, and with a very smooth to a strongly ridged and rugose or verrucose surface; pericarp consistently fleshy and thick (5–15 mm.), and usually made of two, more or less conspicuously different, carnose layers (epicarp and endocarp) separated by a thin, ligneous membrane (mesocarp), the endocarp limited by a firm epidermis inside, the inner wall of the shell, the epicarp sometimes differing in color and firmness, rich in mucilaginous cells, limited outside by the hard epidermis of the fruit, the mesocarpic membrane sometimes reduced to isolated bundles of fibers or lacking, the endocarp also sometimes lacking.

Seeds (20–40) usually arranged in 5 rows, but sometimes when large arranged in 4 or 3 rows, the five radial walls initially separating the 5 cavities in the earlier stages reabsorbed long before the maturation of the fruit; seeds ovoid, ellipsoid, amygdaloid, more or less complanate through mutual pressure or almost round in cross section, variable in size (20–40 mm. long, 12–20 mm. broad), the integuments brown, subcoriaceous, the surrounding pulp white, sweet, the cotyledons white, purplish, violet, or intermediate in color.

Theobroma cacao is variable in its characters, especially with regard to the color, size, and shape of the parts of the flower and the fruits. These are variations to be expected of an ancient crop spread throughout a very wide area.

Based on some of these more or less consistent variations, Bernoulli described three species, *T. pentagonum*, *T. leiocarpum*, and *T. saltz-*

mannianum, and Chevalier *T. sphaerocarpum*. The shape of the fruit is the main defining character, except for *T. saltzmannianum*, which was based on petal characters, probably from an abnormal specimen. The few floral characters given for the other three species are irrelevant or inconstant. *Theobroma pentagonum* is defined by having elongate, gradually and acutely narrowed, warty pods which are strongly pentagonal and 5-ridged; it has white seeds. It was described from the Atlantic coast of Guatemala and is called "cacao lagarto." *Theobroma leiocarpum* was characterized by ovoid pods, almost smooth, with five very shallow furrows and a glabrous ovary; the color of the seeds was not stated; it was found in plantations on the Atlantic coast of Guatemala, and stated to be rather rare. *Theobroma sphaerocarpum* was described from cultivated specimens on São Tomé island, western Africa, characterized by its nearly spherical, slightly 10-furrowed, almost smooth or slightly rough pods, and violet cotyledons. Schumann considered the three Bernoulli species as mere local variations of *T. cacao* and therefore unworthy of taxonomic consideration. Some authors have followed Schumann in this view, but there is a tendency to accept *T. pentagonum* as a different species, because of its characteristic fruit form and thinner pericarp.

For many years there has evidently been confusion in the taxonomy of cultivated cacaos, the main problem being insufficient knowledge of the wild populations of *T. cacao*. There are many citations of places in Central and South America where *T. cacao* is said to have been found wild, which may have been true in some cases, but not in others where we may be dealing with the remains of abandoned plantations. The discovery of wild cacao by Stahel in the rain forests of Mamaboen Creek in Surinam (confirmed later by Myers) and a few other places very distant from populations, is very significant; the cacao is of the Amelonado type. Ogilvie also found it in abundance on Black Creek, a branch of the Essequibo River, and along the Berbice River in British Guiana. He found it along the Rupunumi River at Rewa and Quitaro Creeks, at Kuduwiní Kassikedju or Dewar Wow, etc., on the upper Essequibo River, and also on the Quitari River (according to Myers). Robert Schomburgk also cited wild cacao in several places in British Guiana on the Cutari, at the head of the Correntyne River, and also at Quitaro, and Richard Schomburgk found it on the Upper Pomeroon River. Wild cacaos also have been found, according to Stahel, in the Upper Oyapok in French Guiana (Myers), all of the Amelonado type, implying that this population of the Guiana highland area westwards to the Amazon valley may have been the home of this cultivated variety. In Brazil there has been found wild cacao near the Guianas and, according to Ducke, at the upper Rio Branco, northeast of Obidos, and at Francez

on the middle Tapajóz; he adds that the area of spontaneous *T. cacao* includes a greater part of the Hylaea and that it is of the form "*leiocarpum*." Preuss (1901, p. 247) found wild cacao in eastern Ecuador, also of the Amelonado type. Huber found spontaneous cacao in the upper Purus river, and along the Río Ucayali, Peru. Pound also claimed to have found spontaneous cacaos in the upper Amazon basin. The spontaneous cacao trees found by the Anglo-Colombian Expedition in the forests of Caguán (Caquetá) and Río San Miguel offer some doubt about their indigenusness. I found myself, in 1939, in the rain forests of Río Guaviare wild trees of *T. cacao*, tall and well developed, but we have to be cautious in accepting them as indigenous, because the Guaviare River is said to have had more extensive plantations on its banks in earlier times. An interesting find was made in British Honduras by Sampson, who encountered wild trees of the Criollo type in the Southern forests. In Mexico, Miranda recently found a completely indigenous cacao tree in a forested region of Chiapas (Selva Lacandona), very distant from any population; the natives (Lacandones indians) reported that other trees of such cacaos are found scattered; this cacao has a somewhat scandent stem and produces small, elongated, pointed, slightly 10-ridged and rugose fruits. Standley and Steyermark (Fl. Guat. 426) say that in the lowlands of Guatemala sometimes cacao is found more or less wild in the forest, especially in Alta Verapaz, and that it is not improbable that it is native in the wet North Coast region.

Many forms of the cultivated cacaos have received local or regional names which after the many introductions of cultivars from one country to another have brought confusion to the complicated system of cacao types. Morris was the first to make a classification of cultivars, arranging them in two main groups: Criollo and Forastero. Hart (see page 396) modified this, making three groups (Criollo, Forastero, and Calabacillo), later separating *T. pentagonum* (cultivar "Lagarto") into another group, as a different species from *T. cacao*. The classification of Hart has been followed by many authors of cacao treatises until recent times when van Hall, simplifying, went back to the basic two groups of Morris: Criollo and Forastero.

Pittier, a botanist with much experience both in Central and South America, recognized the existence of two different, original, spontaneous forms of cacao, Criollo with elongated, ridged, pointed fruits and white cotyledons, and Forastero, with short, roundish, almost smooth fruit and purplish cotyledons; he believed that they corresponded with two different species, *T. leiocarpum* generally spread throughout tropical South America, where it is still found spontaneous, and *T. cacao*, spontaneous in Central America and which was the

source of the prehistoric cultivation and selection of cacao, all of the Criollo type, in Mexico and Central America. Introduction of Criollo types in South America and West Indies and conversely of the smooth type into West Indies and Central America created the cross-varieties which multiplied with the years. Although there is much speculation in this, the theory is a workable and reasonable one, because the available historical data favors the recognition of the earlier Central American and Mexican cacaos as being of the Criollo type. The finding of spontaneous cacao of this type in Chiapas and British Honduras also supports this theory. Another favorable fact is the uniformity of the Venezuelan Criollo, supposed to have been introduced from Central America to Venezuela in the earlier times of the Spanish conquest.

Soria, after visiting (1961) important plantations in Mexico where new Forastero types have been abundantly introduced in recent times, recognized that in Mexico before 1900 varieties of the Criollo type almost exclusively were cultivated. He observed in large, old (more than 50 years) plantations a great variation in the Criollo type, but the seeds were always white and the pods, variable in shape, were always pointed, with surfaces varying from tuberculate to rugose, from light green, through green, to reddish; the trees were small, slow growing, and often with fewer branches (5-3 in each whorl) than is normal in the species; the petal-laminas are bright yellow.

Pittier's theory was very much welcomed by botanists and cocoa experts; Chevalier supported it, and Ducke also in its basic idea. Cheesman adhered to it at first (1932), but later (1944) developed a new theory that all cultivated Criollo cacaos came "from an offshoot of a general cacao stock in the headwaters of the Amazon carried over the Andes into southern Colombia, and developed many of their present characters in association with man." But historical knowledge at present can only closely relate cacao to Central American man, especially to the Mayans and not to the South American Indians. Central American Indians undoubtedly developed the art of planting and selecting of cacao through several thousands of years, finally obtaining the high quality produce which the Spaniards found at the time of the conquest.

It may be assumed that in early times a natural population of *Theobroma cacao* was spread throughout the central part of Amazonia-Guiana, westward and northward to the south of Mexico; that these populations developed into two different forms geographically separated by the Panama isthmus; and that these two original forms, when isolated, had sufficiently consistent characters to be recognized as subspecies. As they intermingle readily by crossing, giving fertile

and robust hybrids, they cannot be considered distinct species. Both types in cultivation have originated many mutations, some of them persistent, thanks to ecological adjustment, selection, and isolation. Because the cultivation and selection has been very active for some thousand years in the Central American-Mexican area, it is in these areas where we find the richest variety of forms. When the subspecies (with their different forms) interbred the products gave the great and confusing variety of existing types.

Another theory is that most of the stable forms of cacao might have originated by mutations from a widespread, uniform original specific type. In such a way the forms *pentagonum*, *leiocarpum*, Criollo, Cundiamor, Angoleta, Nacional Ecuador, Trinitario, etc., and their variants could have originated. This theory does not exclude hybridization as a factor in the multiplicity of forms, but its influence would be secondary instead of basic, as postulated by the Pittier theory.

TYPES OF THEOBROMA CACAO.—The only specimen of *T. cacao* in the Linnaean herbarium is the number 934-1, but this specimen is posterior to the publication of *Species Plantarum* (1753), since it bears the annotation "Pl. Surin. 1775. p. 13." The type has to be sought among the bibliographic references of Linnaeus. In *Species Plantarum*, Linnaeus refers to *Hortus Cliffortianus*. At my request, Mr. Sandwith was kind enough to examine the *Hortus Cliffortianus* herbarium at the British Museum and found no specimens of *Theobroma* in it. However, *Hortus Cliffortianus* page 379 seems to give a key to the matter, where Linnaeus writes "Flores a nullo bene depicti, multo minus descripti sunt, . . . Sloane mihi inspiciendi copiam fecit, . . ." and gives the quotation "Hist. Jam. pl. 160." Linnaeus was especially preoccupied with the flowers; he wanted to know exactly the structure in order to be able to place *Theobroma* in the right place in his sexual system; the previous literature did not give him the answer, and neither did the Sloane plate. However, from the above paragraph we may infer that Sloane sent him flowers at his request, surely very few, which may be the reason why there are none of them in the Linnaean herbarium; from Sloane's flowers Linnaeus found the floral structure of *Theobroma* by himself and drafted his diagnosis. The original flowers (surely dissected) having disappeared, the corresponding specimens in the Sloane Herbarium have to be considered the isotype. Messrs. Dandy and Sandwith found the specimens in the Sloane Herbarium at the British Museum. Mr. Sandwith writes: "We found the corresponding specimen in the Sloane Herbarium and it is obviously the source of (in fact part of) the plate, though not identical; there are leaves, detached flowers, frag-

ments of fruit and one seed; it is the vol. 5 p. 59." There is the possibility that Sloane lent Linnaeus these specimens, but even if this were not the case, we may assume that Linnaeus used flowers taken from this specimen which would thus be an isotype; therefore, the sheet page 59, volume 5, of the Sloane Herbarium is to be chosen as lectotype for the flowers and leaves. According to Sandwith and Dandy "there is also what appears to be a duplicate, leaves only, in the Plukenet Herbarium volume of Herb. Sloane. The leaves of both specimens are reddish brown and glabrous beneath with reticulate tertiary veins."

Sloane's plate 160 is a paratype, but another even more important paratype is Tournefort's plate 444. Tournefort is the only reference given by Linnaeus in his original description of the genus in *Genera Plantarum* (1754), and its citation precedes the reference to Sloane in *Hortus Cliffortianus*. I propose it as the lectotype for the fruit, because the Tournefort drawing is perfectly defined, leaving no doubt that the characters are of the Criollo type. On the other hand, the fruits shown on Sloane's plate 160 are not unquestionable, even though they are very pointed; they are among the variations found in Criollo populations. But the reasons which compel me to consider the flower specimens in the Sloane Herbarium as the lectotype do not apply to the fruit, the origin of which may have been different from the origin of the flowers and leaves, for Sloane collected in several places and countries. A fruit typification by the Tournefort plate fits well the definition of *T. cacao* L. *sensu stricto* given by Pittier and later authors. It is obvious that all these authors described cultivars and that the cacao described by the earlier authors was of the type Criollo, as can be inferred from the illustrations, and also from the descriptions of Hernandez, Pison, Plukenet, Merian, Weinmann, Tournefort, Catesby, and Gaertner.

SYNONYMS.—*T. pentagonum* Bernoulli was characterized by the shape of the fruit and by smaller flowers. Last character is inconstant but the fruit form is a very particular one and constant, fruit always easily recognized. This type was described in vivo by Bernoulli from the Atlantic coast of Guatemala; there is no type specimen of the fruit, but it was well drawn (*Pl. 2, fig. III*) and the drawing may be considered the type. It is my belief that *T. pentagonum* is just a cultivar. It crosses easily with other forms of cacao giving intermediate products. Gross morphological study also supports this view. The pericarp in *Theobroma* is composed of three visible layers, one of these being more or less consistently woody; in *T. cacao* the woody layer is the middle one, the mesocarp. It seems that in cultivation there is a tendency for the pods to change, the shells

becoming thinner in the best quality Criollos. This reduction is extreme in *T. pentagonum* which lacks the firm mesocarp and the fleshy endocarp, the whole pericarp being only half as thick as in other cultivars; *pentagonum* trees are also weaker than others. I have no doubt that *pentagonum* is a fixed product of mutation selected for better fruits. I must agree with Soria (1959) when he writes "*Pentagona* is nothing more than one of the extremes in the variability of the complex of types forming the species *T. cacao*." The name must be kept but only at the rank of forma.

Theobroma leiocarpum was also described by Bernoulli from living specimens in cultivation on the Atlantic coast of Guatemala; there are no type specimens of the fruits recorded, and so the published drawing (*Pl. 2, fig. II*) must be chosen as the type. This plant was characterized by a glabrous ovary and smaller flowers (an insignificant feature) and by ovoid, shallowly 5-sulcate, almost smooth fruits. The color of the cotyledons was not mentioned. For a long time this form was identified with the widespread South American "Calabacillo" or "Amelonado" fruit types, especially since Pittier published his theory, it being supposed that the Venezuelan "Calabacillo," with thick-shelled, rounded or ellipsoid, obtuse, slightly 10-furrowed fruits, and violet cotyledons, was *T. leiocarpum*. All workers followed this nomenclature, myself included. It was Cheesman (1944, p. 14) who called attention to the differences between Calabacillo and Central American *T. leiocarpum*. The Bernoulli cacao has thin, ovoid attenuate shells, with only 5 furrows, and plump seeds which are probably white or light violet. Preuss had written previously that the seeds were different. I saw Calabacillo in Nicaragua with very light-violaceous seeds. The recent observation by Soria (1961) in Mexico of the great variety in external form of Criollo in an old plantation of Criollo makes it clear that *T. leiocarpum* is a mere segregate form or mutant from the Criollo type of *T. cacao*, originating in a similar way to *T. pentagonum*. I consider it only as a cultivar.

Theobroma sphaerocarpum was described by Chevalier from cultivation in Isla São Thomé, in the South Atlantic Ocean west of tropical Africa, conforms perfectly with the "Calabacillo" cultivar of Venezuela and other South American plantations. It is an extreme form of the widespread South American subspecies. The type is a preserved fruit in the Museum in Paris. This name has to take the place of the subspecies which Pittier and later authors have called *T. leiocarpum*.

Cacao sativa Aubl. is a nomenclatural synonym of *T. cacao*, and cannot be used as a substitute for the latter. Any imprecision implied by the binomial *T. cacao* is implied also in *Cacao sativa*, and *Theobroma sativum*.

Theobroma sapidum Pittier may well have been unintentionally published as a *lapsus calami* for *T. sativum*; it corresponds to *T. cacao sensu stricto* of Pittier, restricted to the Criollo type. But the binomial is a *nomen nudum*, because it was not formally published, not being accompanied by a description and with no indication of any type.

Cacao minus Gaertn. was published without mention of specimens or locality. It agrees well with some forms of the Criollo type. It cannot be *T. pentagonum* because in *T. pentagonum* the ridges are always very prominent and smooth. The type of the binomial consists of two fruits identical with the original drawing, labeled *Cacao minus*, Gaertner at Paris.

Cacao theobroma de Tussac, *T. integerrima* Stokes, and *T. caribaea* Sweet are nomenclatural synonyms.

Theobroma saltzmannianum was established by Bernoulli, the emarginate petal-laminae being the only difference from *T. cacao* (ligulae lamina anguste obovata, apice truncata emarginata). According to Bernoulli the shape of the ligula was a constant character in *T. cacao* and *T. leiocarpum*; having found at Kew some specimens collected by Salzmann near Bahia, in which he saw the petal-lamina emarginate, he did not hesitate to make a new species. Schumann could not identify this character in any of many flowers collected in Bahia by Salzmann, and inferred that Bernoulli had examined some exceptional, teratological flower. Rombouts in 1948 (Kew Bull. 1948: 104) studied in detail the type specimens at Kew and arrived at the same conclusion as Schumann, that Bernoulli did base his species on an accidental character. Chevalier had already expressed the same view (1946, p. 270). I also can confirm the above opinions after having examined several Salzmann collections at different times and the type specimen in 1954 at Kew.

Theobroma sagittata Pavon was published by Chevalier in his revision (1946: 274) as a microspecies of the complex of *T. cacao*. The binomial, however, is not validly published for lack of the required Latin diagnosis. Moreover, I have identified the type specimen, which is preserved in Paris, as a 3-leaflet fragment of a leaf of *Herrania nitida* (Poepp.) Schultes. *Theobroma hastata*, a name mentioned by Chevalier in the footnote on page 273, presumably is a *lapsus calami* for *T. sagittata*.

The varieties *leucosperma* and *melanosperma* published by Chevalier without reference to any type specimens are fortunately not validly published for lack of Latin diagnoses. It would be very difficult to ascribe these two supposed varieties to any recognized taxonomic entity relying only on the seed color.

COMMON NAMES.—Cacao, cocoa, cacao dulce, cacao criollo, cacao calabacillo, cacao forastero, cacao amelonado, cacao trinitario, cacao lagarto, and many other adjectives according cultivar varieties and regional or local cultivar forms. Also: Bizoya, yagabizoya (*Reko*), deghy (*Otomí*), caocauatzaua (*Zoque*), kako (*Mixe*), cahequa (*Tarasacán*), Chudechu (*Otomí*) in Mexico after Standley; cacahuatl, caca-hoatl, cacahoquahuitl, quauhcacahoatl, mecacahoatl, xochicacahoatl, tlacacahoatl, cacahoacuahuitl, cacaotlquahuitl (*Nauhatl*), kicou, kicob, cuculat, paxoc, cucuh, caco in Costa Rica and Guatemala; cacao chuncho in Peru. For Costa Rica and Chiriquí, Pittier (1902) gives the following Indian names: ko (*Térreba*), koó (*Brunka*), kajo (*Guatuso*), kuá (*Guaimí*), kno (*Penonomé*), doló (*Doraske*), tsirú (*Bribrí*), (*Cabécara*); according to him the *Bribrí* Indians use the following names for some varieties of cacao: murú-uak, tsipá-uak, xi-uak, and betsún-uak; Standley (1937) mentions, also for Costa Rica: kuk (*Rama*), tsirú-kurú (*Cabécara*), kao-krá (*Brunka*) and kau (*Tiribí*). Cacao silvestre, cacao de monte, wild cacao, are names often used in different countries whenever a cacao tree is found apparently spontaneously growing. It is a fact that although the other species have native Indian names, for *Theobroma cacao* only the name "cacao" is recorded from the whole of South America, whereas this species has many indigenous names in Central America.

SUBSPECIFIC DIVISIONS.—A correct classification of all forms will only be possible after careful and extensive genetic research. In the meanwhile we cannot do more than use a provisional, conservative approach, confining the nomenclature to names already used.

The summarized classification given below of cultivated varieties follows Morris, who was the first to give status to the most popular common names of cocoa cultivars; the adaptation in general use made by van Hall is followed in this paper, with few modifications. See also my reviews of Preuss (1901), and Hart (1892, 1900 and 1911) in the Historical Sketch above. The reader will find more extensive information on this subject in special treatises (van Hall, Baker in Urquhart, Hart, etc.).

Key to subspecies and forms of *Theobroma cacao* L.

1. Fruit elongate, claviform, fusiform or ovoid-oblong, tapering and pointed, more or less strongly 10-costate or 5-costate and verrucose; pericarp moderately thick, the woody mesocarp thin; seeds ovoid or ellipsoid, usually rounded in cross section; cotyledons white or yellowish white . . . 7a. subsp. **cacao**
2. Fruit 10-costate 1. f. **cacao**, **lacandonense** and unnamed forms.
2. Fruit claviform, strongly 5-costate, the ridges prominent and smooth, the sides strongly verrucose, the pericarp thinner, lacking the woody mesocarp and endocarp 2. f. **pentagonum**
2. Fruit ovoid, shallowly 5-furrowed, almost smooth, obtusely attenuate at apex 3. f. **leiocarpum**

1. Fruit ellipsoid, almost globose or more or less oblong, rounded at both ends, smooth or slightly verrucose, more or less shallowly 10-furrowed; pericarp very thick, the woody mesocarp firm; seeds ovoid, more or less compressed; cotyledons purplish or dark violet. 7b. subsp. **sphaerocarpum**

7a(1). *Theobroma cacao* subsp. *cacao*

FIGURES 20, 21, 22

Cacao minus Gaertn. 1791.

Theobroma sapidum Pittier, 1932.

Theobroma cacao var. *typica* Ciferri, 1933.

Theobroma sativa var. *leucosperma* Chevalier, 1946.

TYPE.—Sloane Herb. (flowers, leaves) (BM, lectotype); Tournefort *pl.* 444 (fruit-lectotype).

COMMON NAMES.—The leading name is cacao criollo or criollo.

DISTRIBUTION.—Originally from Mexico and Central America, and cultivated more or less extensively in other tropical countries. Corresponds to the Criollo cultivars.

Among the collections examined are:

MEXICO: VERACRUZ: Colonia San Rafael, flowers and pods, January, 1946; forests from Colima to Chiapas, *Olivia Converse* 74 (UC). Fortuño, Coatzacoalcas River, 30–50 m., III 1937, “cacao”; tree 15–25 feet tall, crown fairly dense, trunk branching from base, inner bark reddish or reddish brown, wood light brown, fruit yellow about 8 in. long, 4 in. wide, often cultivated and growing wild in lowlands slightly humid or subject to seasonal floods, (*Ll.*) *Williams* 8457 (F, P).

OAXACA: Santa Maria de Chimilapa, I 1927, “wild cacao,” *Mell* 29 (US).

BRITISH HONDURAS: Stann Creek Valley, Mountain Cow Ridge; tree 5 in. diam., 30 III 1940, “wild cacao,” *Gentle* 3292 (MO, NY, US). Middlesex, 200 ft. alt.; tall tree of upright habit of growth, generally found growing along river banks, fruits dark red, occasional, 19 XI 1929, specimen with fruits, *Schipp* 178 (UC). El Cayo district, Mountain Pine Ridge, 8 V 1931, *Bartlett* 13108 (F, NY).

7a(2). *Theobroma cacao* subsp. *cacao* forma *pentagonum* (Bernoulli) Cuatr., comb. nov.

FIGURES 5, 6, 20, 23

Theobroma pentagona Bernoulli, Uebers. Art. *Theobroma* 6–7, *pl.* 2, *fig.* III. 1869.

Theobroma cacao subsp. *pentagona* (Bernoulli) León in Hardy's *Cacao Man.* 312. 1960.

TYPE.—Bernoulli, *op. cit.*, *plate* 2, *fig.* III, isotype, *Bernoulli* 98 (GOET).

COMMON NAMES.—Cacao lagarto, alligator.

USES.—One of the best quality cacaos known.

DISTRIBUTION.—Only known in cultivation, being probably a mutant cultivar from *T. cacao* L. originally from Central America; mainly cultivated in southern Mexico and Central America, seldom in other areas. It is a weaker variety, for which reason it is being displaced by more robust and disease resistant varieties, in spite of the high quality of its product.

Collections examined (cultivated):

GUATEMALA: Mazatenango, "cult. Marz. 1865 *Theobroma pentagonum* n. sp.?" specimen with two leaves and one seed, *Bernoulli* 98 (GOET, isotype) Retaluleu, Apr. 1878, *Bernoulli & Cario* 3151 (GOET).

COSTA RICA: Turrialba; fruit red, "lagarto" seed white, 7 XI 1961, *Cuatrecasas & Soria* 26540 (US).

COLOMBIA: EL VALLE: Finca Esmirna, "lagarto rojo"; seeds white, 16 X 1961, *Cuatrecasas & Barros* 26004 (US); *ibidem*, "lagarto amarillo"; seeds white, *Cuatrecasas & Barros* 26005 (US).

7a(3). *Theobroma cacao* subsp. *cacao* forma *leiocarpum* (Bernoulli) Ducke, *Rodriguesia* 4:274. 1940. FIGURE 25

Theobroma leiocarpa Bernoulli, Uebers. Art. *Theobroma* 6, 7, pl. 2, fig. II. 1869: (not *T. leiocarpum* of current authors).

Theobroma cacao var. *leiocarpum* Ciferri, Real Accad. Ital. Mem. Cl. Sci. Fis. Mat. e Nat. 4:604. 1933, as to basionym.

Theobroma cacao subsp. *leiocarpum* Cuatr. in Macbride, Field Mus. Publ. Bot. 13 (3A): 654. 1956, as to basionym.

TYPE.—Bernoulli, *op. cit.*, pl. 2, fig. II; isotype, *Bernoulli* 97 (GOET).

COMMON NAME.—Cumacaco (Guatemala).

USES.—A current cocoa of high quality.

DISTRIBUTION.—Atlantic coast of Guatemala and rarely in other parts of Central America and southern Mexico. Only known in cultivation, probably being a mutant cultivar of *T. cacao* L. The commercial type known as "Porcelaine Java Criollo" probably represents this form.

Collections examined (cultivated):

GUATEMALA: Mazatenango, "cult. Marz. 1865, *Theobroma laeve* n. sp.?, " *Bernoulli* 97 (GOET, isotype). Retaluleu, "April 1878, *Theobroma laeve* Bern., " *Bernoulli & Cario* 3152 (GOET).

Theobroma cacao subsp. *cacao* forma *lacandonense* Cuatr., forma nov.

FIGURE 25

Fructus ovoideo-oblongus, acutus, 10-angulatus, 12 cm. longus, 5.3 cm. diam., pericarpio 5 mm. crasso, epidermide dura, epicarpio molli 2-3 mm. crasso, mesocarpio cartilagineo, endocarpio molli circa 2-3 mm. crasso; semina oblonga 20-22 x 14 x 8-10 mm.

Type in the U.S. National Herbarium, No. 2404633, collected near Caribal Lacanjá ("selva lacandona"), northeast of Chiapas, Mexico, in high primary forest (about 50 m. high), 550 m. alt. by F. Miranda (No. 9299); half-vine, about 7 m. tall, with very long branches; trunk 15 cm. diam. The Lacandona Indians call it "cacao."

DISTRIBUTION.—Only known from the type locality. It is a very interesting variety due to the fact that it is a true wild plant and therefore a possible ancestor of the present cultivated cacao.

MEXICO: CHIAPAS: Selva Lacandona, Caribal Lacanja, 550 m. alt. in primary forest, X 1960, *F. Miranda* 9299 (US, holotype).

7b. *Theobroma cacao* subsp. *sphaerocarpum* (Chevalier) Cuatr., comb. nov.

FIGURES 20, 24, 25

Theobroma sphaerocarpa Chevalier, Veget. Util. Afr. Trop. Fr. 4:12. 1908.

Theobroma cacao subsp. *leiocarpum* sensu Cuatr., excl. basionym *T. leiocarpum* Bernoulli.

Theobroma leiocarpum sensu Pittier et auctt., excl. basionym *T. leiocarpum* Bernoulli.

Theobroma cacao var. *leiocarpa* sensu Ciferri, excl. basionym *T. leiocarpum* Bernoulli.

Theobroma cacao f. *leiocarpum* sensu Ducke, excl. basionym *T. leiocarpum* Bernoulli.

TYPE.—São Tomé, *Chevalier*, preserved fruit (P).

COMMON NAMES.—Calabacillo, amelonado, Amazonian forastero, forastero, etc. (South America). Laranja (São Tomé, West Africa).

USES.—A currently used cocoa of variable quality; the original type gives the lowest quality of the cultivated varieties.

DISTRIBUTION.—Native in South America, found spontaneous in the Hylaea from the Guianas and middle Amazonia north and westward to the Andes. Its several cultivars and forms are planted throughout the tropics, especially in South America and Africa. Being hard and robust trees, and fast-growing plants, they are spreading steadily in plantations.

Some of the collections examined are:

BRITISH GUIANA: Mataruki River, upper Essequibo; small riparian tree⁹ *Myers* 5829 (K).

COLOMBIA: META: San Jose del Guaviare, forest on left side of the Guaviare River, 240 m. elev.; fruits 18 x 7 cm., abundant, apparently spontaneous trees, in the lower tree-layer of forest, 14 XI 1939, *Cuatrecasas* 7756 (COL, F, US). Sierra de la Macarena, train between Güejar River and Caño Guapayita, Caño Yerli, 500–600 m. elev.; slender tree 35 ft. tall, 20–28 XII 1950, *Idrobo & Schultes* 784 (COL, US). Ibidem, tree 12 m. tall, 20–28 XII 1950, *Idrobo & Schultes* 940 (COL, F, US). Ibidem, Caño Yerli, dense humid forest; shrub 3 m. tall, 25 XI 1949, *Philipson, Idrobo, & Fernández* 1565, 1569 (BM, COL, US).

AMAZONAS: La Pedrera, Caquetá River, river level; old trees possibly planted long ago and not truly wild on the river banks and islands, pods green, ripening yellow, 20 X 1952, *Baker & Cope* 15 (COL, F, US, TRIN).

CAQUETÁ: Río Caguán, Cartagena; tree 7–8 m., found distant from river bank, white-based pod, smooth and scarcely furrowed, all beans pigmented, 20 IV 1953, *Cope & Holliday* 105 (COL, TRIN, US). Ibidem; tree 8 m., numerous small fruits smooth, distinctly 10-ridged, somewhat pigmented, very dark purple beans, 20 IV 1953, *Cope & Holliday* 107 (COL, TRIN, US).

MAGDALENA: Poponte, in forest of Magdalena valley; tree 30 ft., leaves dark green, flowers yellow, fruit red, 16 XII 1924, *Cyril Allen* 880 (MO). Ibidem; fruit green yellow, *Allen* 881 (MO).

BRAZIL: AMAZONAS: Esperança, at mouth of Rio Javary, in noninundatable rain forest; small tree, flowers whitish, spontaneous "cacao," 25 IX 1942, *Ducke* 1095 (IAN, MG, MO, NY, US); ibidem, *Ducke* 23976 (US). "B." Constant,

inundatable ground; tree; "cacau silvestre," 9 V 1945, *Fróes* 20882 (IAN, NY); ibidem, *Fróes* 20573 (IAN, NY). Rio Solimoes, on an island below Tabatinga; rain forest, slightly inundatable, small tree, flowers white, spontaneous "cacao," 24 IX 1931, *Ducke* 23970 (P).

PERU: LORETO: Río Ucayali, Laguna de Canchahuaya, 28 X 1898, *Huber* 1392 (MG). A specimen collected by Asplund near Tingo Maria (No. 13408) may well represent a new species. I did not study this, the material having been lent to Dr. Schultes, Botanical Museum, Cambridge.

The cultivars of Cacao are grouped as follows:

Fruit elongated and pointed, warty, 10-furrowed, with 5 ridges more prominent than the alternate, or only 5, sometimes almost smooth and only attenuate not pointed; shell medium thick, easy to cut; seeds usually rounded in cross section, white or yellowish white inside, and slightly bitter in taste. (Figs. 5, 20, 21, 22, 23.) . . CRIOLLO
Fruit ellipsoid, rounded at both ends or somewhat narrowed toward the apex, rather smooth, with 10 more or less marked furrows; shell thick and harder to cut; seeds usually flattened, violet inside, bitter in taste. (Some varieties with deep furrows or warty surfaces, and pale violet or white beans, being intermediate forms with Criollo. (Figs. 5, 6, 20, 22, 24, 25.) FORASTERO

CRIOLLO Morris (1882, pp. 12, 13). This is the type developed and propagated since prehistoric times in Central America and southern Mexico and which later acquired importance in western Venezuela (cacao Caracas). It comprises the best qualities of cocoa, but the plants are vulnerable to diseases. Criollo is widely cultivated throughout the tropics, the following cultivars being especially known by the growers: Venezuela criollo, Nicaragua, Java, Ceylon, Samoa, Madagascar, Surinam, and Porcelaine Criollos. See van Hall for more information. Among the Criollos has to be included "Alligator" or "Lagarto" mentioned above as *T. cacao* f. *pentagonum*. It seems to me that "Porcelaine Criollo" corresponds to *T. cacao* f. *leiocarpum*. Figs. 5, 20, 21, 22, 23.

FORASTERO Morris (1882, pp. 12, 13). This group of cultivars was divided by Hart into two: Calabacillo and Forastero, the former containing the most typical, shortly ellipsoid, smooth forms. It comprises the hardiest, easiest and fastest growing types, but also those with lower qualities of cocoa; most Forasteros are an interbreeding product of Calabacillo and Criollo and their segregates. Some varieties have developed a good combination of characters. They originated and spread in South America and Trinidad, especially in the Amazon and Orinoco Valley. The most common known types of Forastero are the four listed by van Hall: Angoleta, rather deeply ridged and warty, about twice as long as broad, with a wide base; Cundeamor, strongly ridged and warty, narrower than half of its length, rather acute at the apex, constricted above the base; Amelonado, oblong, ellipsoid, obtuse, rather smooth with rather shallow

furrows and not constricted above the base; Calabacillo, shortly ellipsoid or almost round, the surface smooth with very shallow furrows. Figs. 5, 6, 20, 22, 24, 25.

The *Trinitarios* also are Forasteros with features intermediate to Criollo, being variable in shape and in seed characters. They probably originated by interbreeding in the Venezuelan Orinoco basin, from which they were introduced to Trinidad where they acquired new genes from old Criollo plantations and developed extensively. Later they were brought to Venezuela (receiving the name Trinitario), to Ceylon, and more recently to other countries. Trinitarios are cocoas with well-balanced conditions of hardness and quality of product. Cacao Nacional of Ecuador is another special Forastero of superior quality. (See van Hall, Baker, etc.)

At the Eighth Inter-American Cacao Conference (1960) an "International Register of Cacao Cultivars" was established, to be organized under the chairmanship of Dr. B. G. D. Bartley, of Trinidad.

Section 4. *Telmatocarpus*

Theobroma sect. *Telmatocarpus* Bernoulli, Uebers. Art. *Theobroma* 11. 1869.

FIGURE 4

Sect. *Bubroma* subsect. *Telmatocarpus* (Bernoulli) Pittier, Rev. Bot. Appl. 10(110):779. 1930.

Petal-lamina lacking. Petal-hood 5-nerved. Stamminodes long-caudate, flagelliform, ovate-enlarged at base, flexuose in aestivation. Filaments 3-antheriferous. Fruit ovoid, ellipsoid or globose, the pericarp thick, costate-nervate-reticulate and lacunose, pilose, or tomentulose, the endocarp rigid, thin-woody. Leaves beneath puberulous or subglabrous. Germination hypogeous. Inflorescences axillary on trunk, small, the peduncles solitary or 2 or 3. Main axis sympodial with pseudoapical growth; orthotropic shoots from axillary buds of the terminal jorquette. Primary branching ternate.

Type species: *Theobroma microcarpum* Mart.

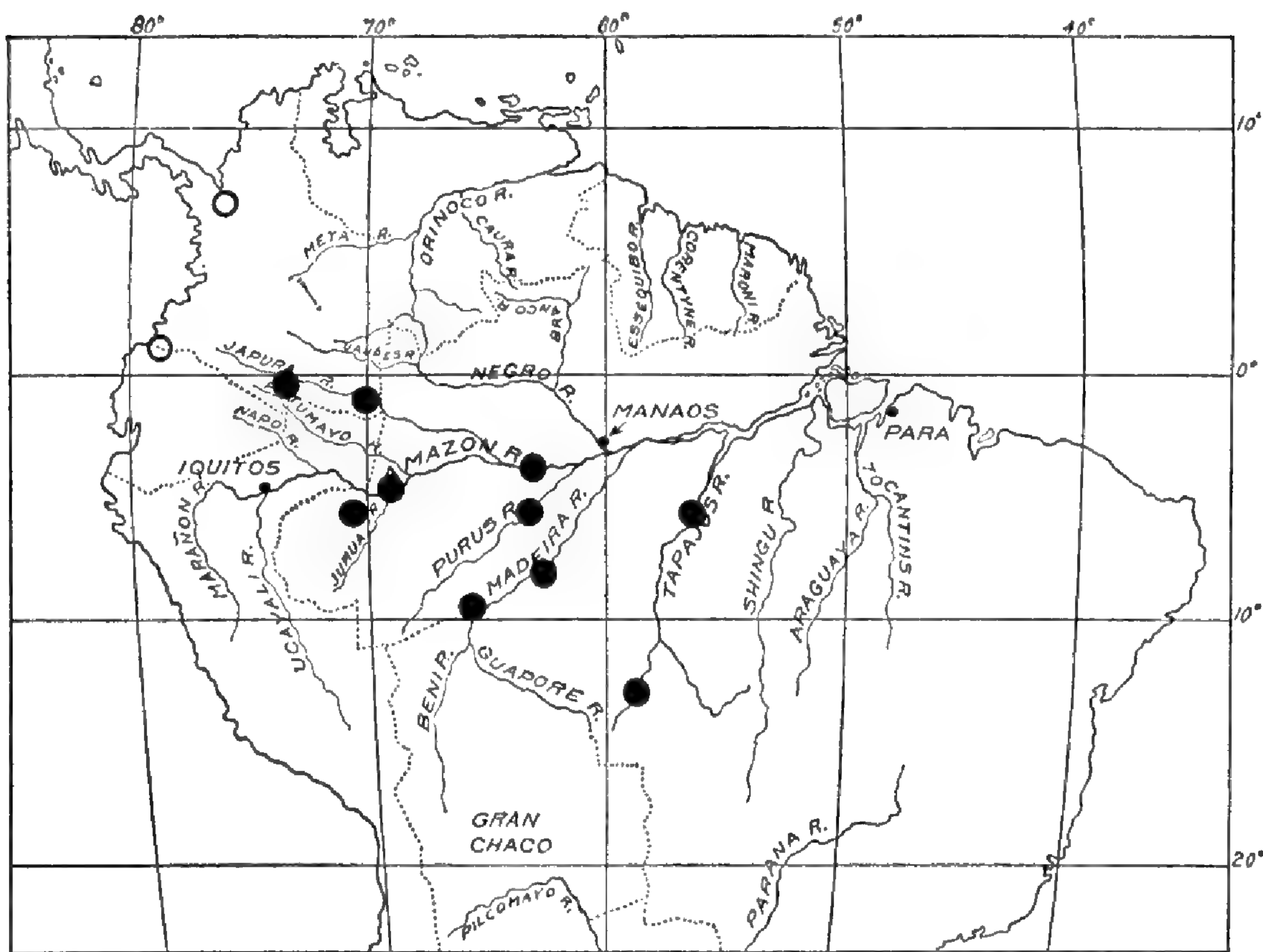
8. *Theobroma gileri* Cuatr.

FIGURES 5, 6, 26, 27, 28, 29; MAP 7

Theobroma gileri Cuatr. Rev. Intern. Bot. Appl. 33:562, fig. 1. 1953; Baker, Cope & al. (1954) 13, fig. 19; León (1960) 316, 315. fig.

TYPE.—Esmeraldas, Ecuador, *Manuel Giler* 162 (flowers), 168 (fruits).

Small tree up to 14 m. high; growth pseudoapical; trunk 20 cm. in diameter, brownish, the bark orange in section, the wood white, rather hard; primary branches ternate-verticillate, light brown, warty lenticellate, glabrous; terminal branchlets thin, the hornotinous stellate-puberulous or pubescent; stipules narrowly subulate, minutely stellate-pubescent, 5–8 mm. long, deciduous.



MAP 7.—Geographical distribution of *Theobroma microcarpum* ● and *T. gileri* ○, the two vicariant species (eastern and western of the Andes) of the sect. *Telmatocarpus*.

Leaves distichous, thin-coriaceous; petioles 3–5 mm. long, mediocre, subterete, stellate-tomentulose, 3–5 mm. long; blade elliptic-lanceolate, narrowed and caudate at apex, asymmetrically rounded at base, entire, 6–22.5 cm. long and 1.5–8 cm. broad (usually 7.5–13 x 2–4 cm.) including the acumen, this acute, 12–25 mm. long, shining above, sparsely stellate-puberulous when young, glabrous or subglabrous when adult except for the midrib, sparsely callous-granulate, the midrib and secondary nerves conspicuous, with scattered appressed stellate hairs beneath, these more copious on the main nerves, but the prominent midrib stellate-tomentulose with smaller stellate hairs, the 5 or 6 secondary nerves each side filiform, conspicuously prominent, arched-ascending, near the margin decurrent and anastomosing, the transverse tertiary nerves prominent, the lesser veins prominulous loosely reticulate.

Inflorescences on tubercular growths on trunk and on the branches, the cymes few-flowered, often reduced to one flower, the axis very short, knotty, bracteate; peduncle erect, filiform, 5–25 mm. long, 3-bracteolate at apex, the pedicel 7–8 mm. long, somewhat thickened toward the apex, scattered pilose; sepals ovate-lanceolate, rather thick, reddish or purplish, glabrous inside, greenish or ochraceous and stellate-tomentulose outside, minutely tomentulose at margin,

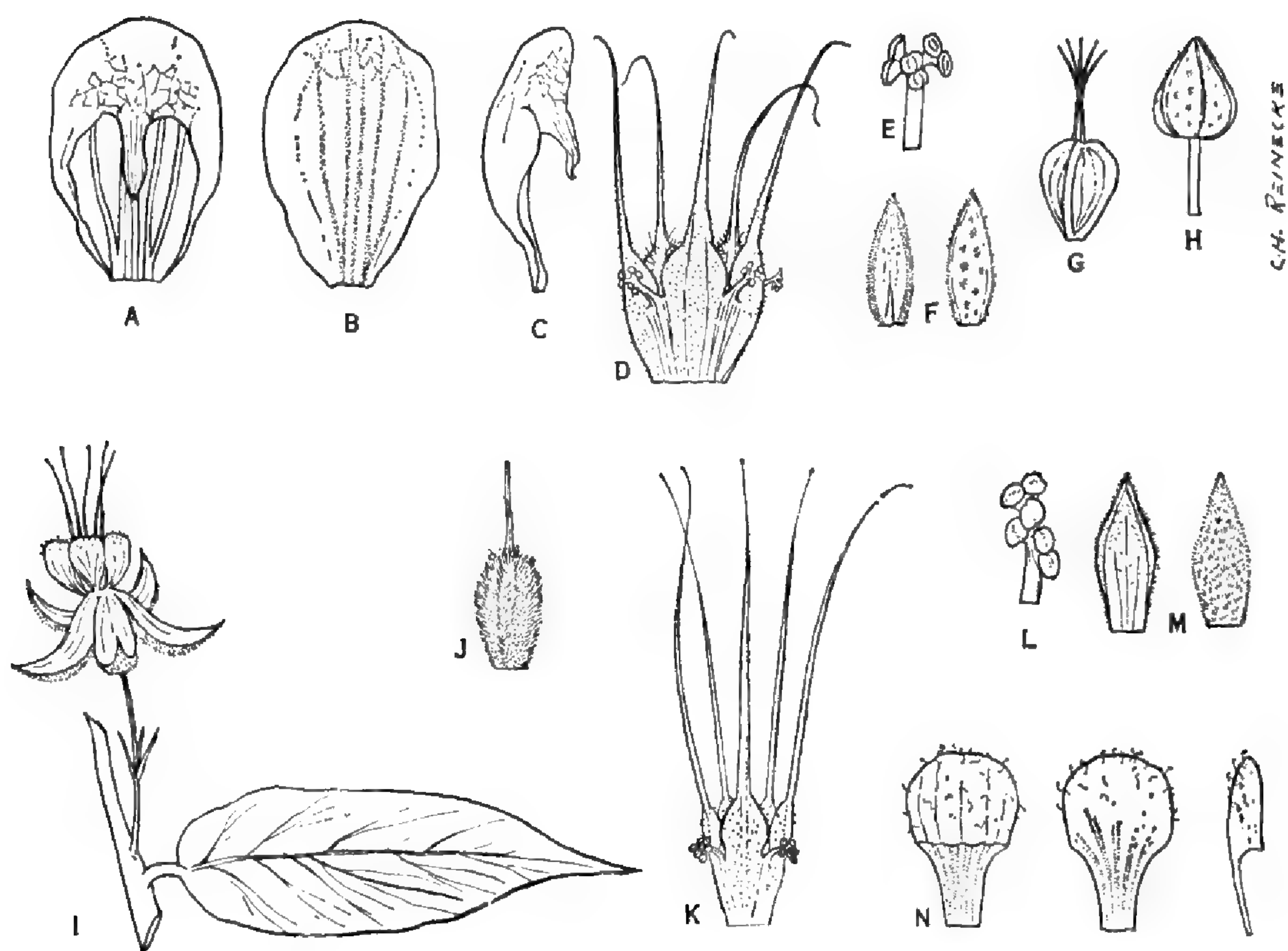


FIGURE 27.—A-H, *Theobroma microcarpum* (Ducke 21045): A, B, C, petal from inside, outside, and laterally, $\times 5$; D, androecium, $\times 5$; E, stamen, $\times 10$; F, sepal from inside and outside, $\times 2$; G, pistil, $\times 5$; H, bud, $\times 2$. I-N, *T. gileri* (Giler 162): I, flower on branch; J, ovary, $\times 5$; K, androecium, $\times 5$; L, stamen, $\times 10$; M, sepal from inside and outside, $\times 2$; N, petal from inside, outside, and laterally, $\times 5$.

united 1–1.5 mm. at base, about 6 mm. long, 3 mm. broad; petal-hoods purplish-red obovate, very narrowed in the lower third, rounded-cucullate, muticous or emarginate at apex, with no appendix, sparsely covered with slender hairs above, with 5 prominent minutely pilose nerves inside, 3–3.2 mm. long, 2.2 mm. broad; androecium purplish red, the tube about 1.2 mm. high, minutely puberulous; staminodes about 7 mm. long, the base laminar, ovate, 1 mm. long and wide, with minute, thick hairs, suddenly narrowed at apex into a subulate, flexuous, flagelliform, glabrous appendix about 6 mm. long; filaments white, rather thick, glabrous, shortly trifurcate, triantheriferous; anthers bilobate, the thecae ellipsoid; ovary ovoid or ellipsoid 5-angulate, densely stellate-tomentose; styles glabrous, about 1 mm. long, coherent.

Fruit ovoid or ellipsoid at maturity, 7.5–11 cm. long, 7.5–9 cm. broad, brownish green or olivaceous, appressed stellate-tomentose, with 5 longitudinal prominulous ribs and irregularly, loosely, reticulate prominulous nerves, the intermediate surface shallowly depressed; pericarp 1 cm. thick, with a pelliclelike epicarp, a thick carnose, very mucilaginous mesocarp, and an inner, 1 mm. thick, coriaceous,

ligneous, hard endocarp, inside with a sweet, flavorous, ochraceous-white pulp surrounding the seeds; seeds ovoid or ovoid-oblong, 2.5–3 cm. long, 1.8–2 cm. broad, 1.5 cm. thick, usually 20–25 in a pod, the

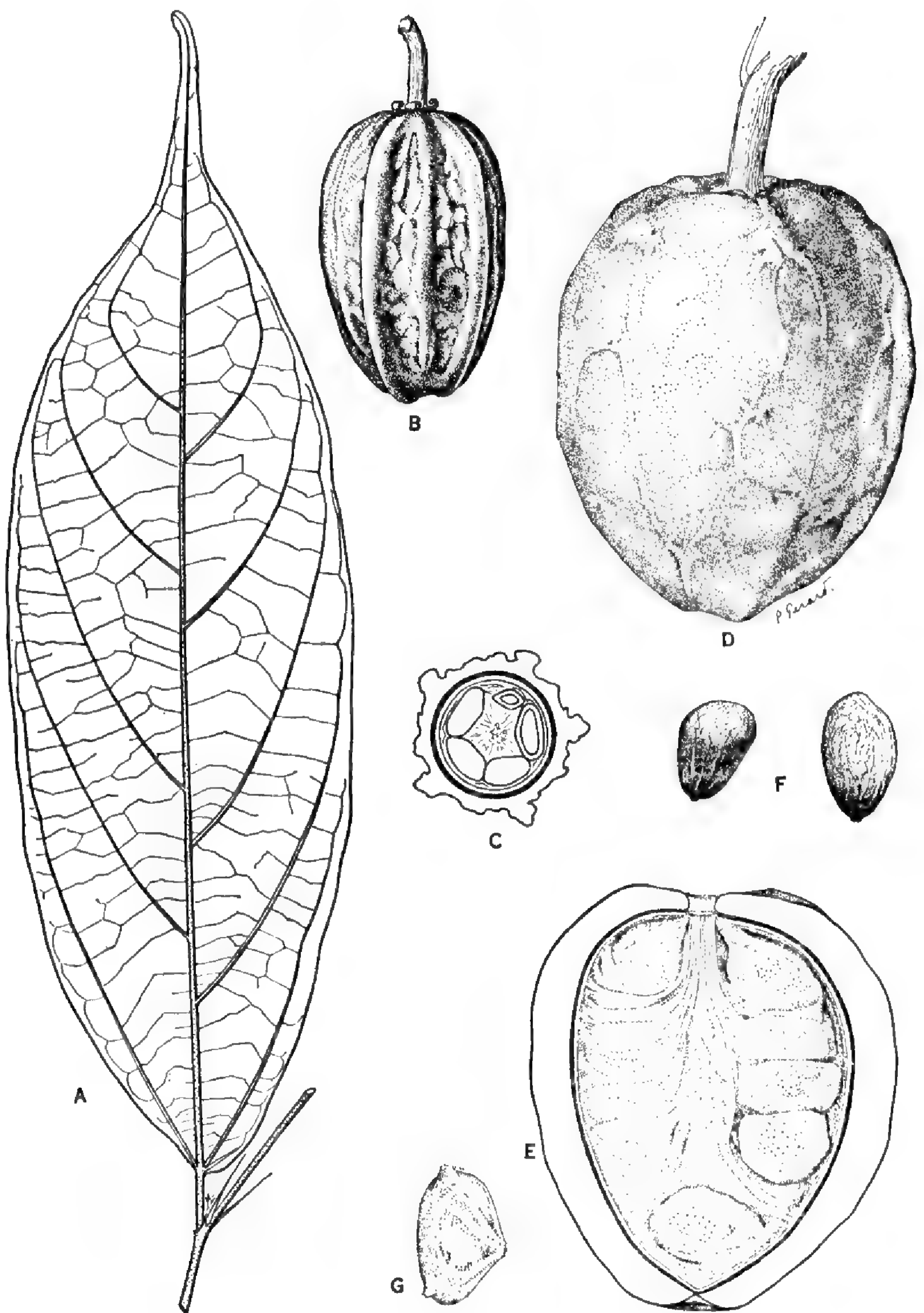
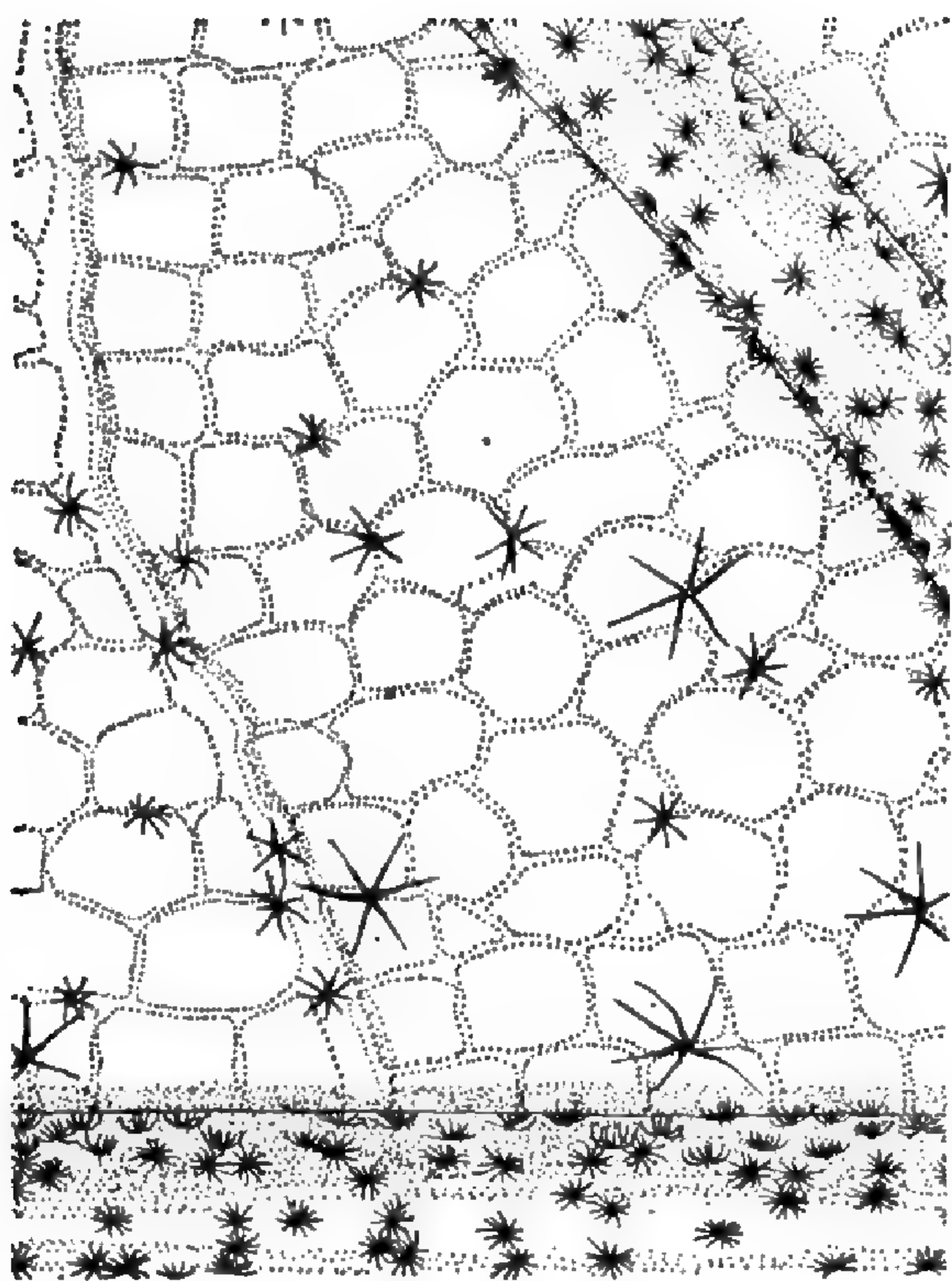
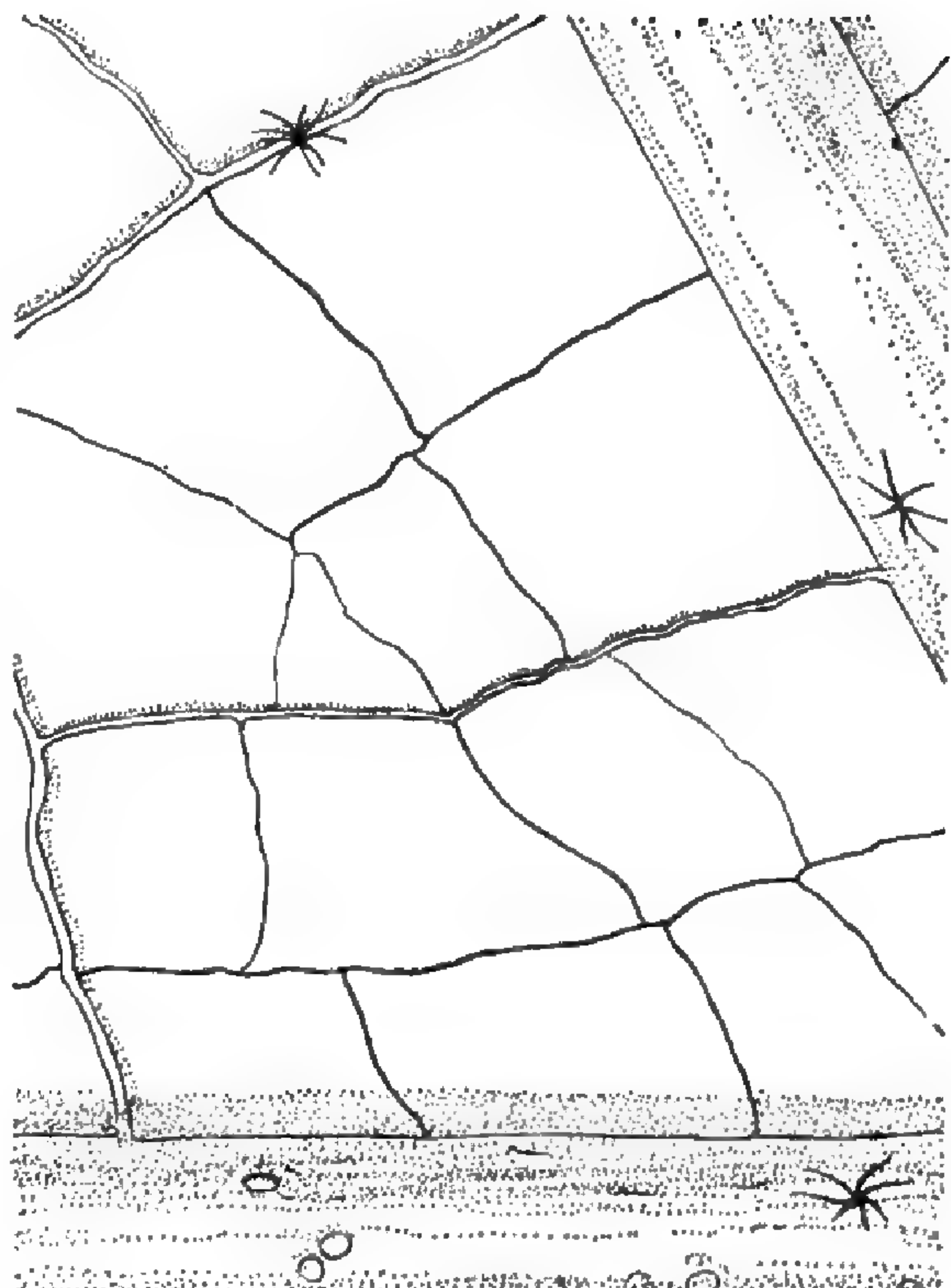


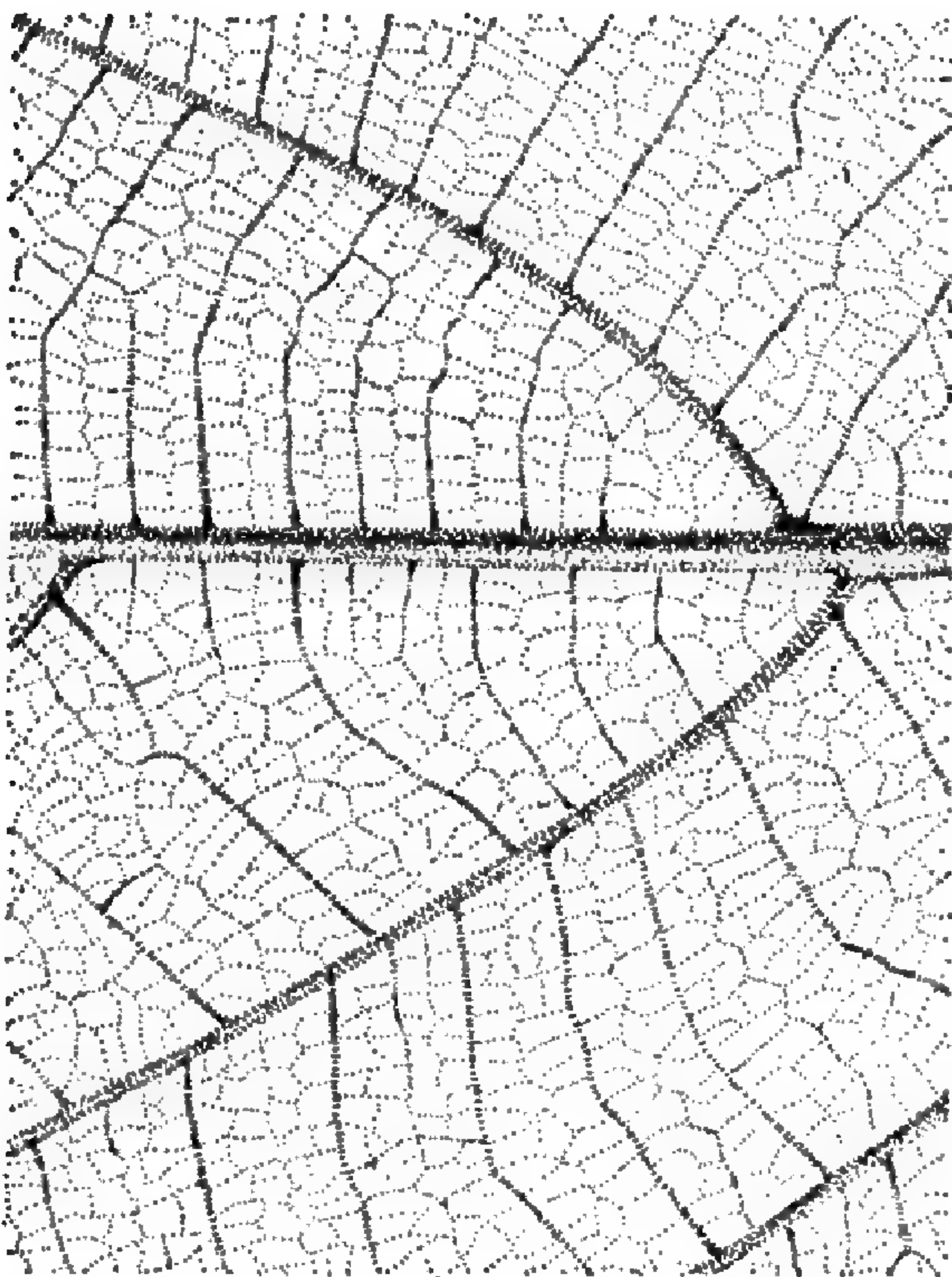
FIGURE 28.—*Theobroma gileri* (Giler 162, 168): A, leaf, $\times 1$; B, young, ribbed fruit, $\times \frac{1}{2}$; C, transection of same; D, mature fruit, $\times \frac{1}{2}$; E, long. section of same; F, two seeds stripped from pulp, $\times \frac{1}{2}$; G, seed with its pulp, $\times \frac{1}{2}$.



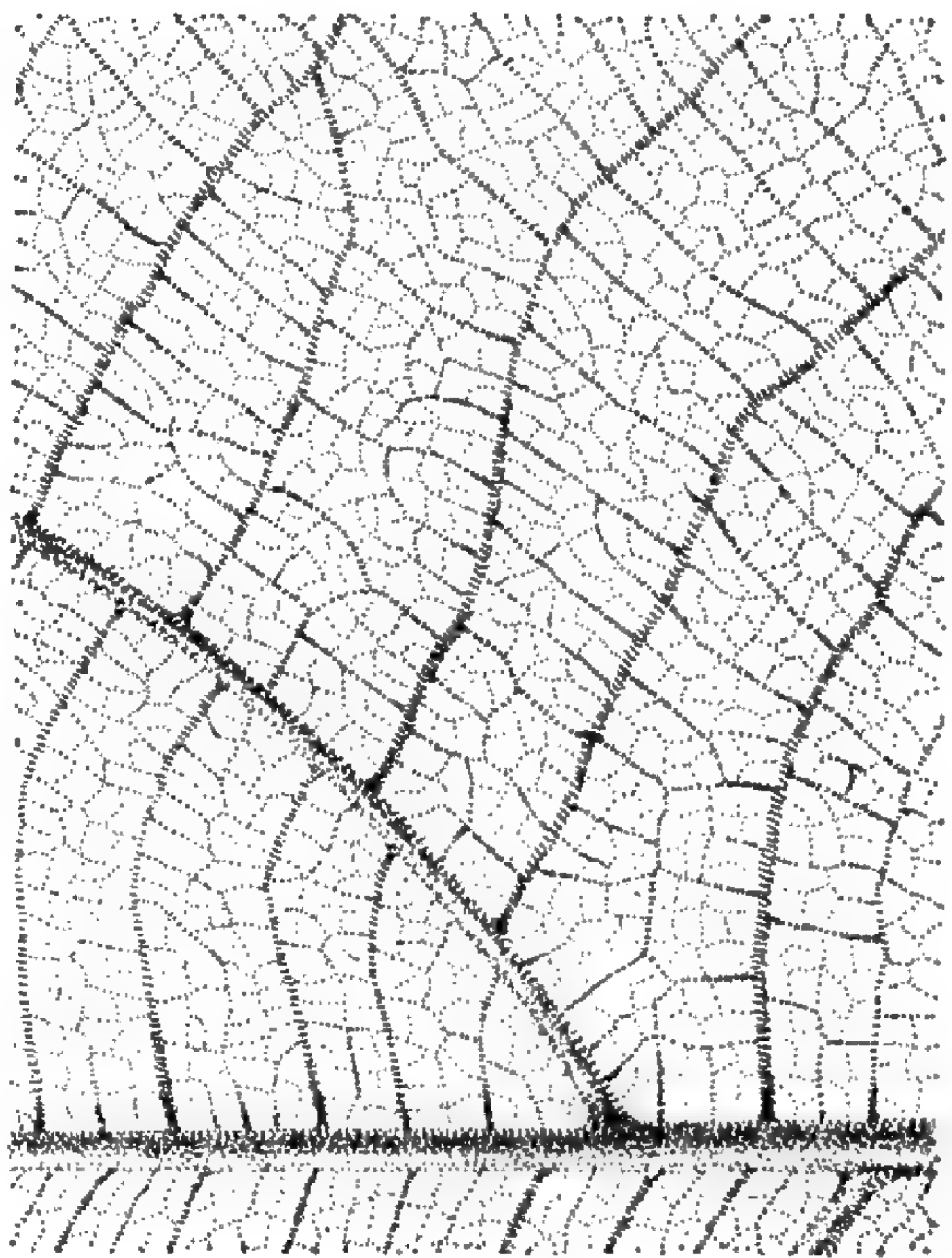
A



B



C



D

FIGURE 29.—A, B, Detail of indument on the underside of the leaf in: A, *Theobroma gileri* (Giler 162); B, *T. microcarpum* (Krukoff 1644). C, D, detail of nervation at the underside of the leaf in: C, *T. angustifolium* (Allen 6259); D, *T. subincanum* (Cuatr. 7277). A $\times 35$, B $\times 25$, C and D $\times 2$.

cotyledons white, when fresh condition.¹ The juvenile fruits are ellipsoid or oblong-ellipsoid, with 5 very strong, protuberant ribs and 5 less prominent ribs, these sometimes becoming covered by the fleshy mesocarp at maturity, but often mature fruits are strongly 10-ribbed; fruiting peduncle 2-3 cm. long, about 6 mm. in diameter; germination hypogeous.

The fruits of *T. gileri* are conspicuously larger than those of *T. microcarpum*, its Amazonian vicariant; they are more oblong-ellipsoid or more oblong in shape. The young fruits have 10 very prominent and thick ribs, 5 of them much stronger than the alternate, and a coarse reticulum between the ribs. In a perfect, healthy, mature fruit, the surface becomes slightly 5-ribbed and shallowly reticulate-lacunose, the fleshy tissue of the mesocarp having filled up the spaces between the ribs, as is shown in *fig. 28*. But often mature fruits keep the 10-ribbed, strongly reticulate shape of the young stage, looking very similar then to the fruits of *T. bicolor*. Both kinds and different sizes of fruits are usually seen on the same tree. The trees are commonly 8-10 m. high in heavy rain forests. The growth is pseudo-terminal, that is to say, by shoots produced above the terminal whorl of branches or jorquette. The branching is normally verticillate (ternate) but often *T. gileri* develops adventitious, upright shoots which give irregularity to the branching. Fungus diseases may have some influence in this. Already in 1953 Patiño wrote: "Unfortunately, in spite of the abundance of trees, this species does not seem to offer much commercial prospects, because almost all fruits we found were diseased. I sent specimens to Quito to identify the responsible fungi," and he says further: "Almost all fruits we saw suffer a disease which hardens the mucilaginous tissue making it compact and hardening the seeds, many are covered by a mashy down, partly or the whole." I have seen myself the same, very recently near Villa Arteaga. Baker et al. wrote: "Seeds of this species were sent to Trinidad but arrived in a decomposed condition. The fungus *Monilia roreri* Ciferri was found infecting fruit of this species."

COMMON NAMES.—Chocolate de monte.

USES.—Natives used to chew or eat the pulp, which is sweet and aromatic. They prepare also a chocolate which is said to have a good taste (Patiño).

DISTRIBUTION.—Restricted to the rain forests of western Colombia and northwestern Ecuador.

COLOMBIA: ANTIOQUIA: Villa Arteaga; tree 10-12 m., 15-18 cm. in diameter at base, flowers not seen but borne in cushions on trunk and main branches, fruit about 9 x 7 cm., ridged and reticulate, said to be yellow at maturity, jorquette

¹ Holdridge reports them purplish when cut.

symmetrical, 22 VII 1953, *Holliday & Bartley* T./163 (TRIN, US). Ibidem; tree about 10 m., dry fruit 0–9.5 x 7–7.5 cm., no flowers, 24 VII 1923, *Holliday & Bartley* T./167 (TRIN, US). Mutatá, in virgin forest on slope above Villa Arteaga, 250 m. alt.; small tree, 8 m. tall, 18 cm. DBH, cauliflorous and ramiflorous, sepals greenbacked but reddish inside, petals dark blood red, base of central column reddish, fruit 10-furrowed, elliptical in long section, about 15 cm. long, seeds purplish inside when cut, 23 IX 1959, *Holdridge* 5133 (US). Ibidem, about 150 feet alt.; tree 12 m. tall, 6–20 II 1953, *Schultes & Cabrera* 18695 (US). Villa Arteaga, Las Caucheras, Villa Agraria, rain forest, 200 m. alt.; tree 15 m. tall, stem 8 cm. in diam., crown narrow, primary branches ternate, abundant inflorescence-cushions (now dry, woody) on the trunk and oldest branches, many old fruits on trunk and fallen, and some green ones, hanging, leaves chartaceous, firm, fruits 10 x 7 cm., 10 x 6.5, 11 x 7.5, 11 x 8 cm., 2 X 1961, *Cuatrecasas & Willard* 26167 (COL, US).

ECUADOR: ESMERALDAS: Río Mira, Guadual, near Piguambí camp, 27 VII 1953, *Giler* 162 (holotype, F, 1423965; isotypes, F, US). Ibidem (fruits), *Giler* 168 (paratype, F). Ibidem, *Giler & Patiño* 164, 165, 166 (H. Cuatr.). Probably at Río Mira; fruit collected by *Acosta Solís & Giler* 12392, 12423 (F). Santo Domingo de los Colorados, cultivated from seeds brought from Lita, 27 IX 1957, *Jorge León* 4832 (TURRI).

9. *Theobroma microcarpum* Mart.

FIGURES 26, 27, 29, 35; MAP 7

Theobroma microcarpum Mart. in Buchn. Repert. 35: 24. 1830; Linnaea, Litt. Bericht. 32. 1831; Bernoulli (1869) 11, pl. 5; Schumann in Mart. (1886) 75; Jumelle (1899) 32, fig. 17; De Wildeman (1902) 95; Huber (1906a) 273; Ducke (1925) 131; (1940) 271, pl. 1, fig. 4; (1953) 14; Chevalier (1946) 277; Addison & Tavares (1951) 25, pl. 9, 12, fig. 5; Baker, Cope & al. (1954) 12, fig. 11; León (1960) 316, 321, fig.

TYPE.—Brazil, Rio Negro, *Martius*.

Small tree up to 10–20 m. high; stem 20–30 cm. in diameter; growth pseudoapical; crown small; branches much ramose, ternate at least when young, brownish rugulose; branchlets thin, the hornotinous appressed stellate-tomentose, cinereous or pale ochraceous, becoming glabrous in age; stipules narrow, subulate, pubescent, 2.5–4 mm. long, soon deciduous.

Leaves chartaceous, light green; petioles mediocre, subterete, appressed tomentose, when older transversely wrinkled, 4–8 mm. long (in very young specimens longer, up to 15 mm.); blades triplinerved, elliptic-oblong or obovate-oblong, attenuate near the base, rounded or shortly attenuate at apex, abruptly long-acuminate, asymmetrically rounded at base or sometimes rounded one side, the other cuneate, rarely symmetrically cuneate, 6–18.5 cm. long, 2–7 cm. broad, including the acumen, this 0.7–2.5 cm. long, the margin entire, with scattered minute, simple and stellate hairs above and pubescent costa or glabrous throughout, the main nerves filiform, conspicuous, the loose reticulum almost obsolete, with sparse, minute, stellate hairs beneath or subglabrous, the principal nerves more or less minutely tomentellous or glabrate, the costa and the lower pair of lateral ascending nerves

prominent, the other 2–4 secondary nerves each side thin but prominent, ascending, curved near the margin, anastomosing, the slender, transverse tertiary nerves prominulous and the minor reticulate veins less prominulous, but conspicuous.

Inflorescences axillary or extra-axillary on young leafy branchlets, the cymose clusters extremely small, bearing 1–3 flowers, the woody primary branches short, knotty, bearing ovate, amplexant bracts, 0.6 mm. long and wide; peduncles rather thick, 0.5–1 mm. long, tomentulose, with 3 subulate, deciduous bracteoles at apex, these 0.6–1 mm. long; pedicels 0.5–1 mm. long, moderately thick, tomentulose; buds ovoid, acute, 4.5 mm. long, 3 mm. broad, with 5 whitish, minutely tomentulose lines and scattered, minute stellate hairs.

Sepals thick-membranaceous, lanceolate, acute, united about 1 mm. at base, 5–6 mm. long, 2 mm. broad, with scattered, minute, stellate hairs outside, minutely, whitish tomentulose at margin, with conspicuous midrib and sparse, mediocre, flexuous, glandular hairs inside; petal-hoods pale brown, thick-membranaceous, glabrous, oblong-obovate, rounded-cucullate and acuminate at apex, the acumen triangular, shortly bidentate, exappendiculate, the 5 nerves rather thick, prominent and minutely papillose inside, often confluent into pairs near the base; androecium red or reddish, the tube about 1.5 mm. high, 10-furrowed, minutely pilose; staminodes minutely pilose with a rather thick, oblong-ovate concave base, this 2.5 mm. long and 1 mm. broad with fine flexuose hairs inside, topped by a subulate, flexuose tail 4–5 mm. long; filaments rather thick, 1 mm. long, shortly 3-furcate, triantheriferous; cells of anthers ellipsoid, about 0.4 mm. long; ovary 1.5–1.8 mm. long, pyriform, glabrous or sparsely, minutely stellate-pilose, sharply 10-furrowed-costate; styles 5, united in the lower fourth, rather thick, acute, glabrous.

Young fruit ellipsoid (± 3 cm. long), strongly 10-ribbed, with 5 very thick and prominent, dorsal, shortly pinnate costae, and 5 smaller, commissural ones; mature fruit 6.5–7 (–9) cm. long, 5.5–6.5 cm. broad, green yellowish, puberulous, ellipsoid-globose, conspicuously 10-ribbed, the surface between the ribs shallowly alveolate, the exocarp thick, carnose, padding the hollows between the lignose underlayer, when dry the ribs and the lignose reticulum become extremely marked and prominent; seeds more or less compressed, ovoid, 12–14 mm. long, 18–20 mm. broad, and 11–12 mm. thick; fruiting peduncle thick, robust, 4–8 mm. long and broad; cotyledons hypogeous at germination.

COMMON NAMES.—Cacauí, cacaúrana, cacao rana, cacau bravo, cabeça de urubú (Brazil). Cacao de monte (Colombia). Me-tró-ree-moo-ee (*Karihona*, Upper Apaporis); bóo-e (*Mirana*, Caquetá River) (Angl-Col. Cocoa Exp., Baker, 1952).

USES.—None recorded on the use of its sweet scentless pulp or the seeds.

DISTRIBUTION.—In the southern and western upper Amazon Brazilian region Rios Solimoes, Yapurá, Purús, Madeira, Tapajós, and western Colombia on Caquetá River. (Baker & Cope.) The eastern known limit according to Ducke is Rio Tapajós. The specimens around Belém are cultivated. It is frequent in its area and may become abundant in some places as a significant element of the shadowy under layer of rain forests on elevated ground and in moderately inundatable alluvial lands.

COLOMBIA: AMAZONAS: Río Caquetá, La Pedrera, river level; tall tree 15–20 m., 30 cm. in diam. at base, extensive branch system, jorquettes of seedlings 3-branched, growth continuing from above, flowers small, petals without ligules, fruit abnormal due to attack by *Marasmius perniciosus*, 5 X 1952, *Baker & Cope* 28 (COL, K, TRIN, US). Ibidem; tall tree 15–20 m., native in forest on the riverbank, 7 X 1952, *Baker & Cope* 29 (COL, F, K, TRIN, US). Ibidem; tree 30 feet, 9 inches in diameter, on floodbank, 5 X 1952, *Schultes & I. Cabrera* 17780 (AMES, US). Río Caquetá, Remolino; leaves only from small seedling tree 2.5 m., typical *Theobroma* habit, jorquettes arising symmetrically, 2 V 1953, *Cope & Holliday* T/125 (COL, TRIN, US).

BRAZIL: AMAZONAS: In sylvis ad Costa de Ubicuna et de Camarocoari, fluv. Solimoes, prov. Rio Negro (“Dr. Martius Iter Brasiliensis, 321”), *Martius* Observ. 2890, [884] (M, lectotype, photo F. M. 19643). Ibidem, *Martius* Observ. 2890, [885, 886] (M, isotypes). Lower Rio Yapurá, Jubará matta, 15 IX 1904, *Ducke* 6773 (BM, MG). Basin of Rio Solimoes, Municipality São Paulo de Olivença, near Palmares; tree 60 ft. high, trunk 7 inches in diam., terra firma, high land, 11 IX–26 X 1936, *Krukoff* 8280 (A, BM, F, G, GB, K, LE, MICH, MO, P, S, U, US, USDA). Ibidem; mata, caatinga, “cacao bravo,” arvore pequena, 19 IV 1945, *Fróes* 20750 (IAN, USDA), 34814 (IAN). Basin Rio Madeira, Municipality Humayta, near Livramento, on Rio Livramento on varzea land; tree 50 feet high, “cabeça de Urubú,” 12 X–6 XI 1934, *Krukoff* 6592 (A, BM, F, G, K, LE, MICH, MO, S, U, US, USDA, WU). Ibidem, Municipality Humayta, near Tres Casas, on restinga alta; tree 60 ft. high, 14 IX–11 X 1934, *Krukoff* 6203 (A, F, G, K, LE, MO, S, U, US, USDA, Y). Rio Purus, Bom Lugar; “cacao rana,” II 1904, *Goeldi* 4228 (BM, G, MG). Camatian; high forest lowland, border of creek; tree 7 m. high, 25 cm diam., 24 I 1949, *Fróes* 23963 (IAN, US).

GUAPORE: Porto velho, Entrada de Redagan, Km. 8, Viana, mata derrumbada, terra firme; arvore pequena, 31 V 1952, *Black, Cordeiro, & Francisco* 52–14649 (IAN, UC).

MATO GROSSO: Machado River region, source of the Jatuarana River; tree 3 feet high in terra firma, “cabeça de urubu,” XII 1931, *Krukoff* 1644 (A, BM, F, G, K, MICH, MO, P, S, U, UC).

PARÁ: Belém, Jardim Botânico do Museu Goeldi; medium tree, cultivated, 11 VIII 1942, *Archer* 7551 (F, IAN, K, USDA). Belém, Horto Botânico Pará (cultum proven. Rio Purus, Bom Lugar anno 1904), 25 V 1906, *Huber* 7081 (G, MG). Ibidem; arbor parva floribus rubescentibus, 4 II 1926, *Ducke* 21045 (G, GH, K, S, U, US). Ibidem; arbor parva, floribus pallide brunnescentibus, “cacaohy,” IX 1936, *Ducke* 283 (A, F, K, MO, S, US). Ibidem, 21 VII 1944, *F. C. Camargo* 8 (IAN). Ibidem, 23 XI 1945, *Pires & Black* 742 (IAN). Rio Guama, near Belém, “cacao bravo,” IV 1929, *Dahlgren & Sella* 10 (F, GH). Rio Tapajos, Cachoeira do Mangabal, beira de assahyzal, 7 IX 1916, *Ducke* 16466 (BM, G, MG, P, US).

COSTA RICA: (cult.) Limon, La Lola, experimental station IICA; tree 4 m. tall, narrow crown, eight years old, first flowers this year, 7 XI 1961, *Cuatrecasas* & *Paredes* 26538 (US).

Section 5. Glossopetalum

Theobroma sectio *Glossopetalum* Bernoulli, Uebers. Art. *Theobroma* 11. 1869

FIGURES 1, 3, 4; MAP 2

Sect. *Bubroma* Schum. in Engl. & Prantl. Nat. Pflanzenfam. 3(6):89. 1890.

Sect. *Bubroma* subsect. *Glossopetalum* (Bernoulli) Pittier, Rev. Bot. Appl. 10 (110):779. 1930.

Petal-laminas obovate, spatulate or trapezoid, stipitate. Petal-hoods 7-nerved. Staminodes laminar, petaloid, obovate or broadly lanceolate, curved-reflexed covering the hoods in aestivation, erect or reflexed in anthesis. Filaments 3-antheriferous. Fruit ellipsoid or oblong, smooth or more or less angulate or tuberculate, the epicarp hard, woody, with a tomentose epidermis. Cotyledons hypogeous at germination. Leaves beneath reticulate-nerved, stellate-tomentose. Inflorescences on the main trunk or on the branches. Main axis sympodial with pseudoapical growth; orthotropic shoots from axillary buds of the terminal jorquette. Primary branching ternate.

TYPE SPECIES.—*Theobroma grandiflorum* Schumann.

10. *Theobroma angustifolium* Moçinho & Sessé

FIGURES 6, 25, 29, 30, 31, 37; MAP 8

Theobroma angustifolium Moçinho et Sessé ex DC. Prodr. 1: 484. 1824; Icon.

Fl. Mexicana ex DC. pl. 112; Bernoulli (1869) 12, pl. 6; Schumann in Mart. (1886) 77; Donn. Smith in Pittier, Prim. Fl. Costar. 96. 1898; Preuss (1901) 255, pl. 2,6; De Wildeman (1902) 96, figs. 12,13; Standley (1923) 808; Standley (1937) 687; Chevalier (1946) 282; Standley & Steyermark (1949) 421; Holdridge (1950a) 3; Allen (1956) 342, pl. 26; León (1960) 318, 315, fig.

TYPE.—*Sessé et Moçinho*, Plantae Novae Hispaniae, Herbarium Florae Mexicanae.

Tree 8–26 m. high; trunk up to 30 cm. in diameter, with smooth bark and whitish wood; growth pseudoapical; primary branches ternate; lower branches horizontal, the higher ascending; branchlets when young green ochraceous, densely and moderately appressed tomentose, with very minute, fine, translucent-white stellate hairs intermixed with other mediocre, fulvous or ochraceous, somewhat thicker, stellate hairs, when older more or less glabrate, grayish, rugulose; stipules lanceolate-subulate, acute, broadened at base, above sparsely, below densely stellate-tomentose, 5–7 (–15) mm. long, about 1 (–2) mm. broad, deciduous.

Leaves distichous, thin-coriaceous, rather flexible; petioles moderately thick, densely subappressed tomentose, 6–10 mm. long; blades subobovate-oblong, elliptic-oblong, or oblanceolate, slightly narrowed



MAP 8.—Geographical distribution of *Theobroma angustifolium* ● and *T. simiarum* ○.

to the obtuse and slightly asymmetrical base, attenuate and acuminate at apex, entire or at the upper part slightly sinuate-dentate, 9–25 cm. long and 3–9 cm. broad, including the 1–2 cm. long and 3–5 mm. wide acumen, green above, when adult smooth, glabrous or with few hairs scattered on the costa, this depressed, filiform, the secondary and tertiary nerves little conspicuous, light greenish or cinereous beneath, appressed tomentose, heterotrichous, the surface covered with a dense layer of white, minute, stellate hairs, and additional, more or less copious, larger, ochraceous, stellate hairs with longer rays on the main nerves, the costa very prominent, the 6–8 secondary nerves on each side thinner and prominent, ascending, near the margin decurrent, becoming slender, vanishing, the transverse tertiary nerves, thin, prominulous, 2–5 mm. from each other, the minute reticulum conspicuous.

Inflorescences usually abundant on the branchlets, axillary or extra-axillary, the cymes strongly reduced to a few extremely short 1–3-flowered branchlets; peduncles 0.4–1 mm. long, 3-bracteolate; pedicels erect, rigid, mediocre, densely ochraceous or ferruginous, ebracteate, 5–10 mm. long; bracteoles very minute (1–0.5 mm. long), linear, deciduous; buds globose, 7–8 mm. broad, densely ochraceous tomentose; calyx 8–9 mm. long, reflexed in anthesis, all the sepals united to 3–4 mm. into a cupular base, in the upper part two united

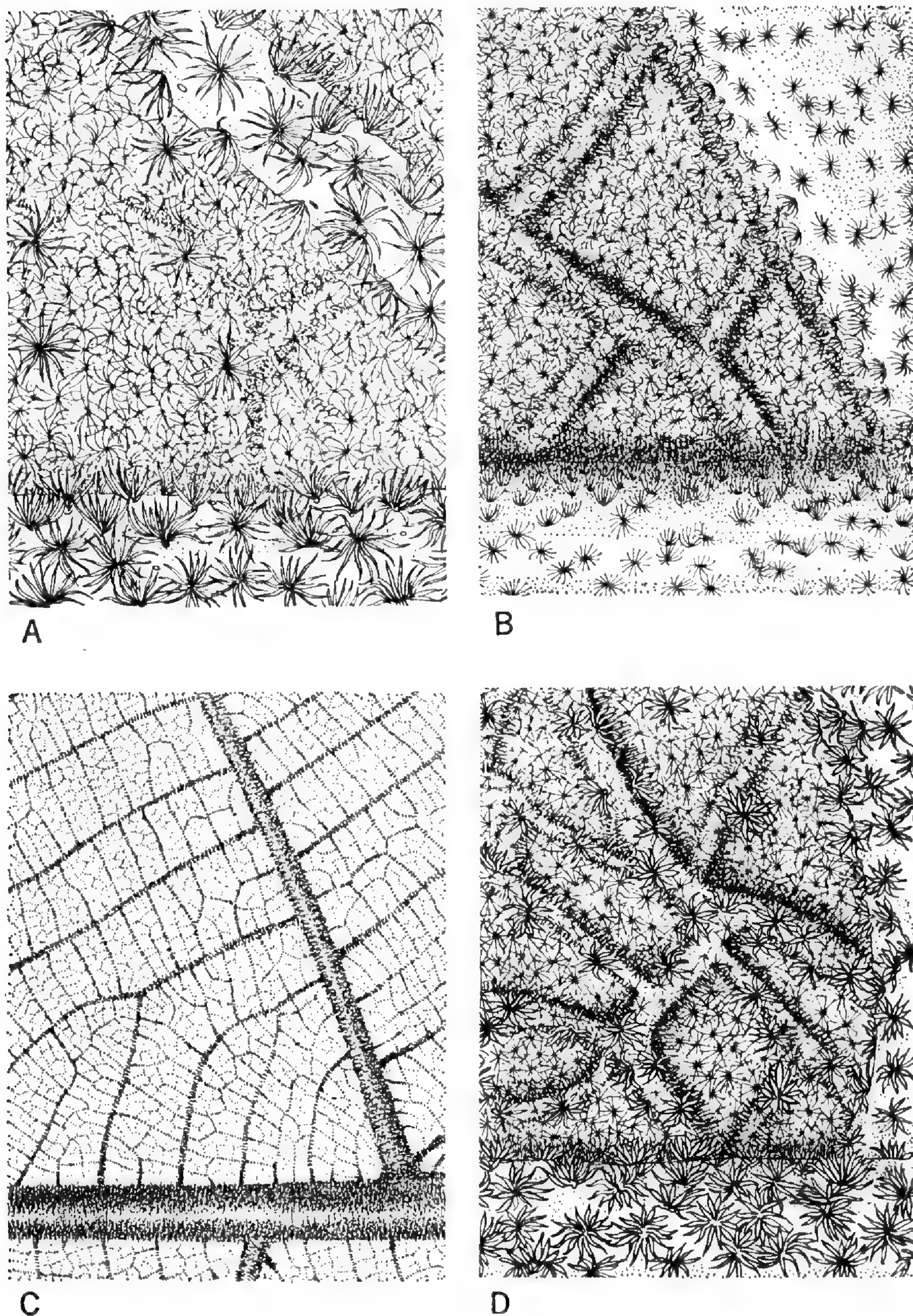
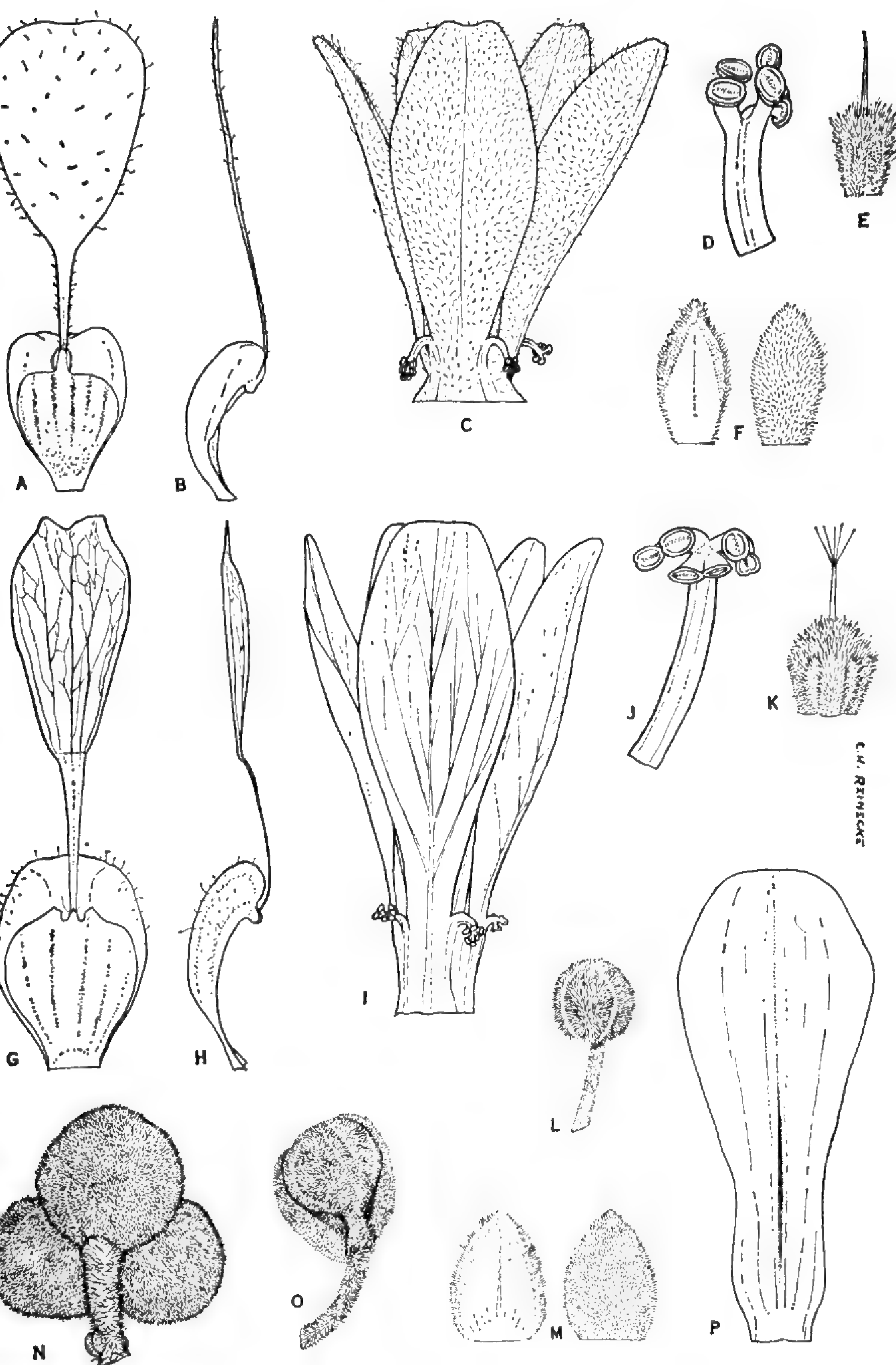


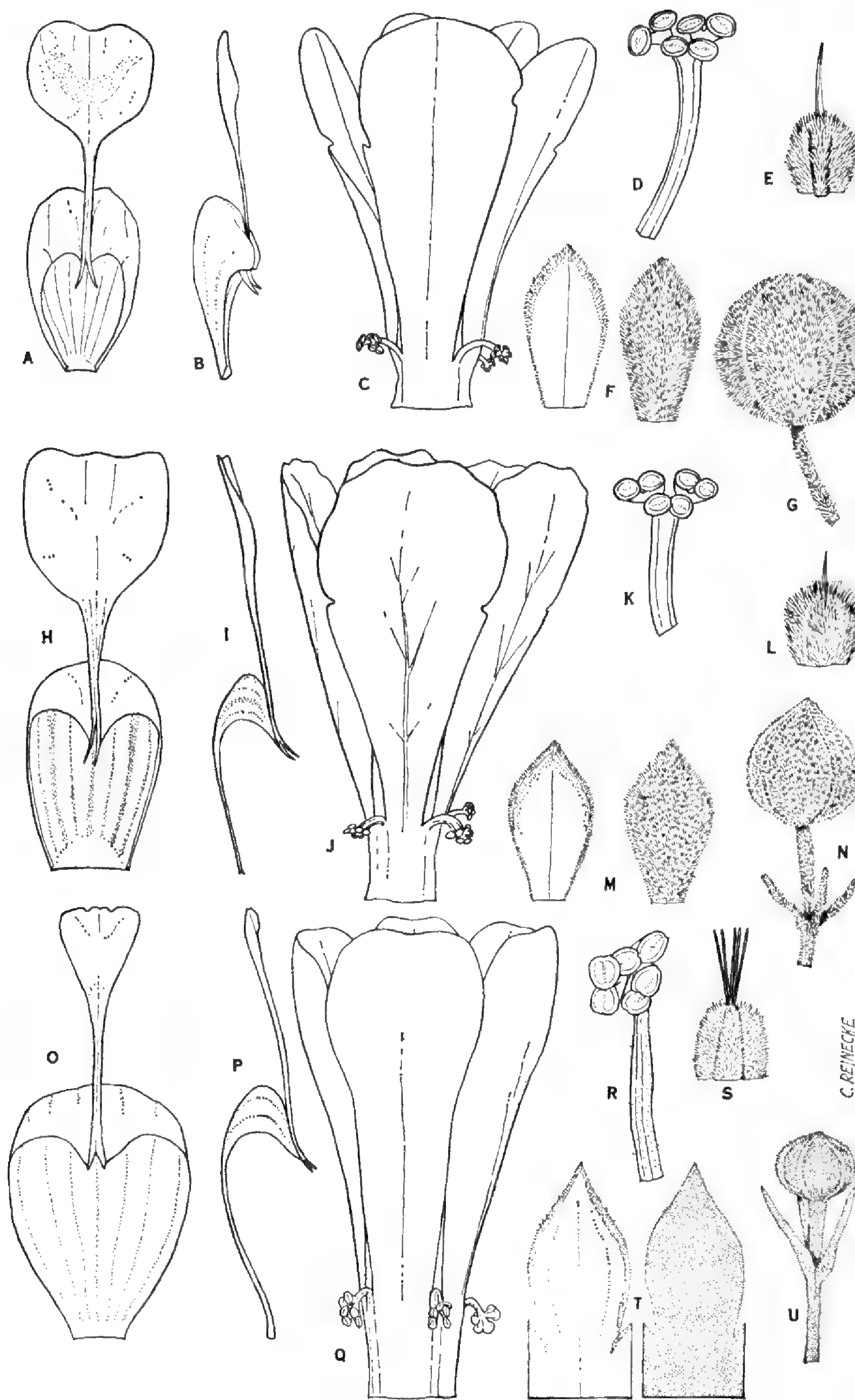
FIGURE 30.—Detail of indument on the underside of leaf in: A, *T. angustifolium* (Allen 6259); B, *T. cirmolinae* (Cuatr. 14897); C, detail of venation in *T. stipulatum* (Cuatr. 21339); D, indument in *T. stipulatum* (Cuatr. 21339). A, B, and D $\times 30$, C $\times 2$.

FIGURE 31.—A-F, *Theobroma nemorale* (Patiño 116): A, B, petal from inside and laterally, $\times 5$; C, androecium, $\times 5$; D, stamen, $\times 10$; E, gynoecium, $\times 5$; F, sepal from inside and outside, $\times 2$. G-M, *T. angustifolium* (Allen 6341): G, H, petal from inside and laterally, $\times 5$; I, androecium, $\times 5$; J, stamen, $\times 10$; K, gynoecium, $\times 5$; L, bud, $\times 2$;



[FIGURE 31]

m, sepal from inside and outside, $\times 2$. n, o, *T. nemorale* (Cuatr. 26007): n, the three bracteoles covering the opening flower, $\times 2$; o, pedicelled bud surrounded by a bracteole, the other two removed. p, *T. chocoense*, staminode, $\times 5$ (Cuatr. 26074).



[FIGURE 32]

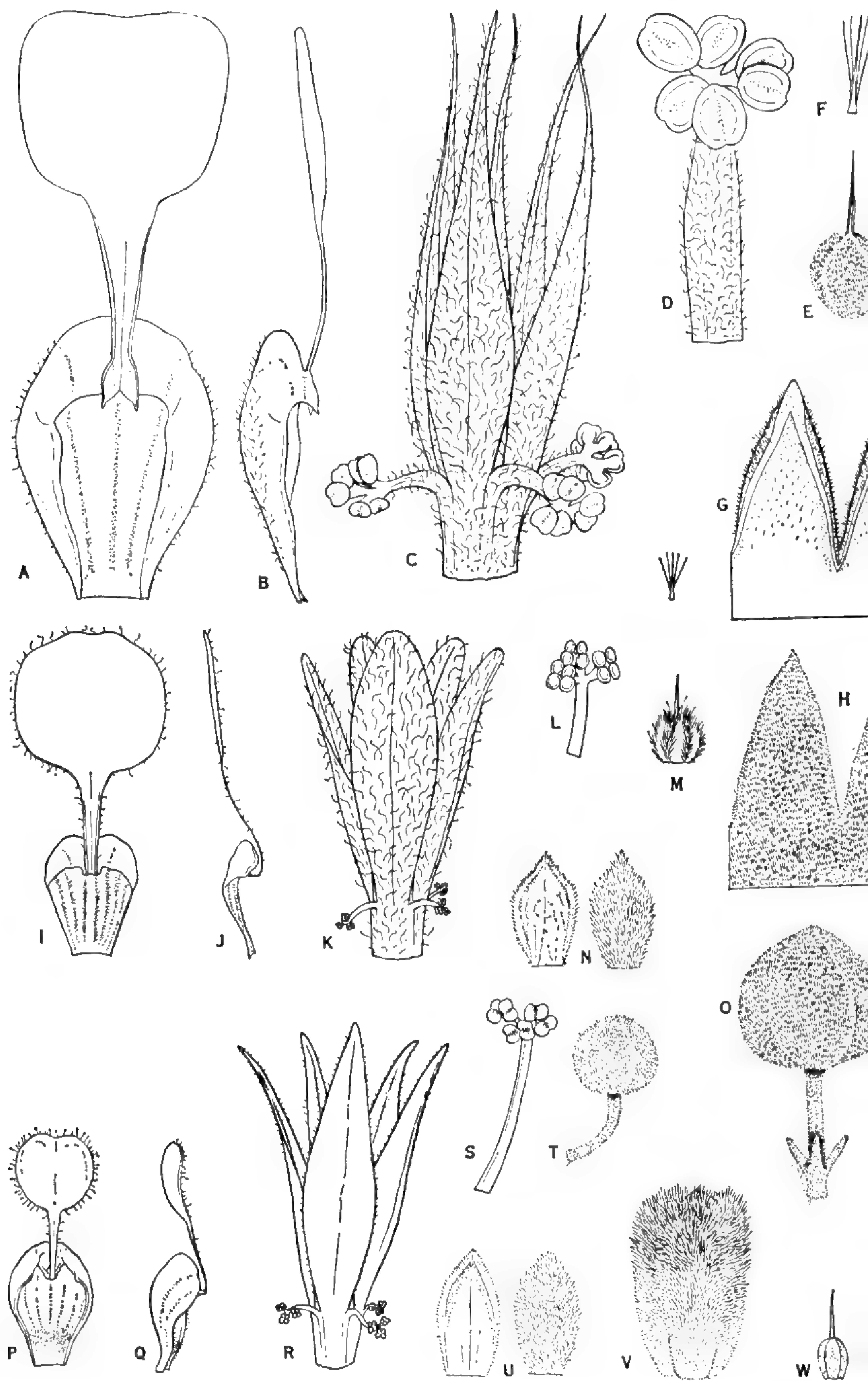
by pairs forming 3 unequal lobes, two of the lobes twice as broad as the third, ovate, rather obtuse, scarcely puberulous and with minute, thick, oblong glandular hairs at the base inside, tomentose, greenish ochraceous or ferruginous outside, each single sepal 4–5 mm. wide.

Petal-hoods thick-membranaceous, yellowish, broadly obovate, rounded-cucullate at apex, 7-nerved with very sparse, thin hairs outside, about 5 mm. long, 4 mm. broad; petal-lamina pedicellate, yellow, thick-membranaceous, 5-nerved and finely veined, subobovate-spatulate, emarginate at apex with 2 ovate or rounded lobes, attenuate towards the base, glabrous, about 5.5 mm. long, 3 mm. broad, the pedicel linear, 3-nerved, attenuate downward, about 4–5 mm. long, 1 mm. wide; androecium tube 2.5–3 mm. long, thick; staminodes laminar, thick-membranaceous, sulphur yellow, glabrous, oblong-obovate, rounded or subspatulate at apex, with marked venation, 8–11 mm. long, 4.2–5 mm. broad, at base 1.2 mm. broad, when in bud curved-reflexed, in anthesis erect; filaments glabrous, thick, curved, 2 mm. long, enlarged and shortly 3-furcate, 3-antheriferous; anther cells globose; ovary obovoid-oblong, about 1.5 mm. long, 5-sulcate, densely stellate-tomentose; styles 2.5 mm. long, united in a rigid erect column 1.5 mm. long, ending in 5 slender branches 1 mm. long.

Fruit unequally oblong-ellipsoid or ovoid-ellipsoid, more or less pentagonal, slightly attenuate at apex, umbilicate and 5-costate at base, very irregularly tuberculate-rugose, densely brown tomentose, the epicarp hard, ligneous, about 1.5 mm. thick, the mesocarp plus endocarp carnose 5–6 mm. thick, the pulp enveloping the seeds thick, juicy, aromatic, edible, 10–18 cm. long, 6–9 cm. broad; seeds 5–7 in each fruit compartment, compressed oblong-ovoid, 26–32 mm. long, 16–19 mm. broad, and 14–16 mm. thick, the cotyledons white; germination hypogeous.

The leaves of *T. angustifolium* are similar to those of *T. nemorale*, but they are narrower, rather lanceolate, and the larger hairs of the double indument beneath are longer with much finer, longer rays than those of *T. nemorale*. Paul Allen (1956) writes about this tree: "The young branches, petioles, and veins of the lower leaf surface are covered with a rather scurfy pale-tan tomentum. The relatively

FIGURE 32.—A–G, *Theobroma stipulatum* (Cuatr. 21339): A, B, petal from inside and laterally, $\times 5$; C, androecium, $\times 5$; D, stamen, $\times 10$; E, gynoecium, $\times 5$; F, sepal from inside and outside, $\times 2$; G, bud, $\times 2$. H–N, *T. simiarum* (Tonduz 7313): H, I, petal from inside and laterally, $\times 5$; J, androecium, $\times 5$; K, stamen, $\times 10$; L, gynoecium, $\times 5$; M, sepal from inside and outside, $\times 2$; N, bud supported by pedicel and 3-bracteolate peduncle, $\times 2$. O–U, *T. cirmolinae* (Cuatr. 14897): O, P, petal from inside and laterally, $\times 5$; Q, androecium, $\times 5$; R, stamen, $\times 10$; S, gynoecium, $\times 5$; T, sepal from inside and outside, $\times 2$; U, pedunculate bud, $\times 2$.



[FIGURE 33]

large, bright-orange flowers are produced in great profusion in several successive flowerings from November until February from the axils of the slender, younger branches, and are followed in August and September by the large, woody, brown-tomentose, cacaolike pendulous pods which are from 4'' to about 7'' in length."

COMMON NAMES.—Cacao de mico, cacao silvestre (Costa Rica), cushta, cacao de la India (Salvador), cacao silvestre (Mexico). Cacao de mico, cacao meco, coca mono (Nicaragua), soró (*Bribi* indians).

USES.—It was stated by Standley (1923) that *T. angustifolium* was much planted in southern Mexico, especially in Chiapas as a source of commercial cacao and that the famous Soconusco cacao was from this species. This statement is very doubtful, for the seeds of *T. angustifolium* are considered at present in that area as of inferior quality without commercial value.

DISTRIBUTION.—This species is often planted in Central America and southern Mexico. It is certainly native in the lowland forests of the Pacific range of Costa Rica (Allen) and nearby Central American countries (Holdridge). Standley and Steyermark (1949, 422) say that the native region of this cacao is unknown, but Tonduz already in 1891 cited it from the forests of Terraba; León (No. 937) writes: "Important tree in the regional forests," and Allen says that "it is locally frequent in lowland forests throughout the area [Golfo Dulce]."

MEXICO: Dirección de Estudios Biológicos, Ord. 34-G823 (MEXU). Herbarium Sessé & Moçino in M, "18-1, Theobroma Simiarum N. Ic," Sessé, Moçino, Castillo, & Maldonado 3618 (holotype, MA; isotype, F, Photo F. M. 48411). Sessé & Moçino s.n. (BM, probable isotype). Copy of the Sessé & Moçino drawing at G (Negative F. M. 30527), plate 112 of the DC. published series.

GUATEMALA (cult.): Retaluleu, April, 1877, Bernoulli & Cario 3188 (GOET, K, S). Mazatenango, III 1865, cult., Bernoulli 95 (NY, BR). Region of Platanares, between Taxisco and Guazacapán (Dept. Santa Rosa), 220 m. alt., wet forested quebrada; small tree escaped here, 3 XII 1940, Standley 79068 (F, US).

SALVADOR (cult.): Sonsonate, "cushta," 1922, Calderón 630 (GH, NY, US). Vicinity of Sonsonate, 220-300 m. alt.; tree 20-30 feet, very dense and narrow crown, flowers on branches, fruit brown, the pulp edible with very aromatic odor, seeds give chocolate, grown here only in finca, "cushta," "cacao de la India," Standley 22317 (GH, MO, NY, US).

FIGURE 33.—A-H, *Theobroma grandiflorum* (Ducke 598): A, B, petal from inside and laterally, $\times 5$; C, androecium, $\times 5$; D, stamen, $\times 10$; E, gynoecium, $\times 5$; F, styles, $\times 5$; G, sepals from inside, $\times 2$; H, sepals from outside, $\times 2$. I-O, *T. obovatum* (Ducke 265): I, J, petal from inside and laterally, $\times 5$; K, androecium, $\times 5$; L, stamen, $\times 10$; M, gynoecium, $\times 5$; N, sepal from inside and outside, $\times 2$; O, bud supported by bracteolate peduncle and pedicel, $\times 2$. P-W, *T. subincanum* (Baker & Cope 32 and Holliday 43): P, Q, petal, from inside and laterally, $\times 5$; R, androecium, $\times 5$; S, stamen, $\times 10$; T, bud, $\times 2$; U, sepal from inside and outside, $\times 2$; V, initiation of fruit, $\times 5$; W, ovary, $\times 5$.

NICARAGUA: Quezalguaque, Dept. of León, *Baker* 2102 (A, AMES, C, GH, G, K, L, MICH, MO, NY, U, UC, US, WU). Chichigalpa, "cacao de mico," II 1900, *Preuss* 1381 (UC). Belén, "cacao meco," "coca mono," or "monkey cocoa," 28 VI 1893, *Hart* 5381 (K, NY, U).

COSTA RICA: GUANACASTE: Upper portion of cañón of Río San José, 460–480 m., 12, 13 II 1930, *Dodge & Thomas* 6399 (F, GH, MICH, MO, UC, US). Nicoya, 300 m. alt., VI 1949, *Lopez* s.n. (F, TURRI). Ibidem, *Pittier* s.n. (US). Hojancha de Nicoya, 20 m. árbol importante en la selva de la región, "cacao de mico," 29 I 1942, *León* 937 (F). Perico, Nicoya, 100 m., I 1954, *León* 4267 (TURRI). Borde du Río Zurquín, 3 1894, *Pittier & Durand* 8536 (P).

LIMON: Cienaguita, near Puerto Limón, 10 m. alt.; small tree with appressed crown, flowers sulphur yellow, VII 1901, *Pittier* 16142 (G, US, WU). La Lola, I.I.A.C.A. experimental station, about 20 m. alt.; tree erect, trunk about 25 cm. diam. at base; pseudoapical growth; primary branches ternate, spreading, persistent; leaves thin-coriaceous but firm, light green and somewhat glaucous and cinereous beneath; young fruits thickly tomentose, axillary flowers abundant, now dry, 6 XI 1961, *J. Cuatrecasas & Paredes* 26537 (US).

PUNTARENAS: Dans le forêt à Terraba, 260 m. alt., II 1891, *Tonduz* 4074 (US). Ibidem; "cacao de mico," II 1891, *Pittier & Tonduz* 4074 (BR, G). Boruca, Diquis Valley, 1891, *Pittier* s.n. (US). Tinoco Station, fairly frequent in swampy forest; tree 80 ft., fruits pendulous, produced from the ends of branches, "cacao de mico," 13 VII 1951, *Allen* 6259 (BH, MO, US). Lowland forest near Palmar Norte; tree 45 feet, flowers bright orange, *Allen* 6341 (BH, F, MO, US). Llanuras de Corredor (Golfo Dulce), III 1897, *Pittier* 11112 (G).

PANAMA: Progreso (Chiriquí); small tree 30 feet, 6 inches in diam., with a fruit like wild cacao except that the husk is smooth like a potato skin, big seeds with white meat inside, 1927, *Cooper & Slater* 242 (F, GH, NY, US, Y). Comarca del Barú, Puerto Armuelles, United Fruit Company farms between Canasco and Cocos, mostly cutover land with some of the original trees still standing, about 100 feet alt.; tree, fruit resembling a cacao pod; leaves pale bluish, green, beneath, 17 VI 1957, *Stern & Chambers* 140 (MO, US, Y).

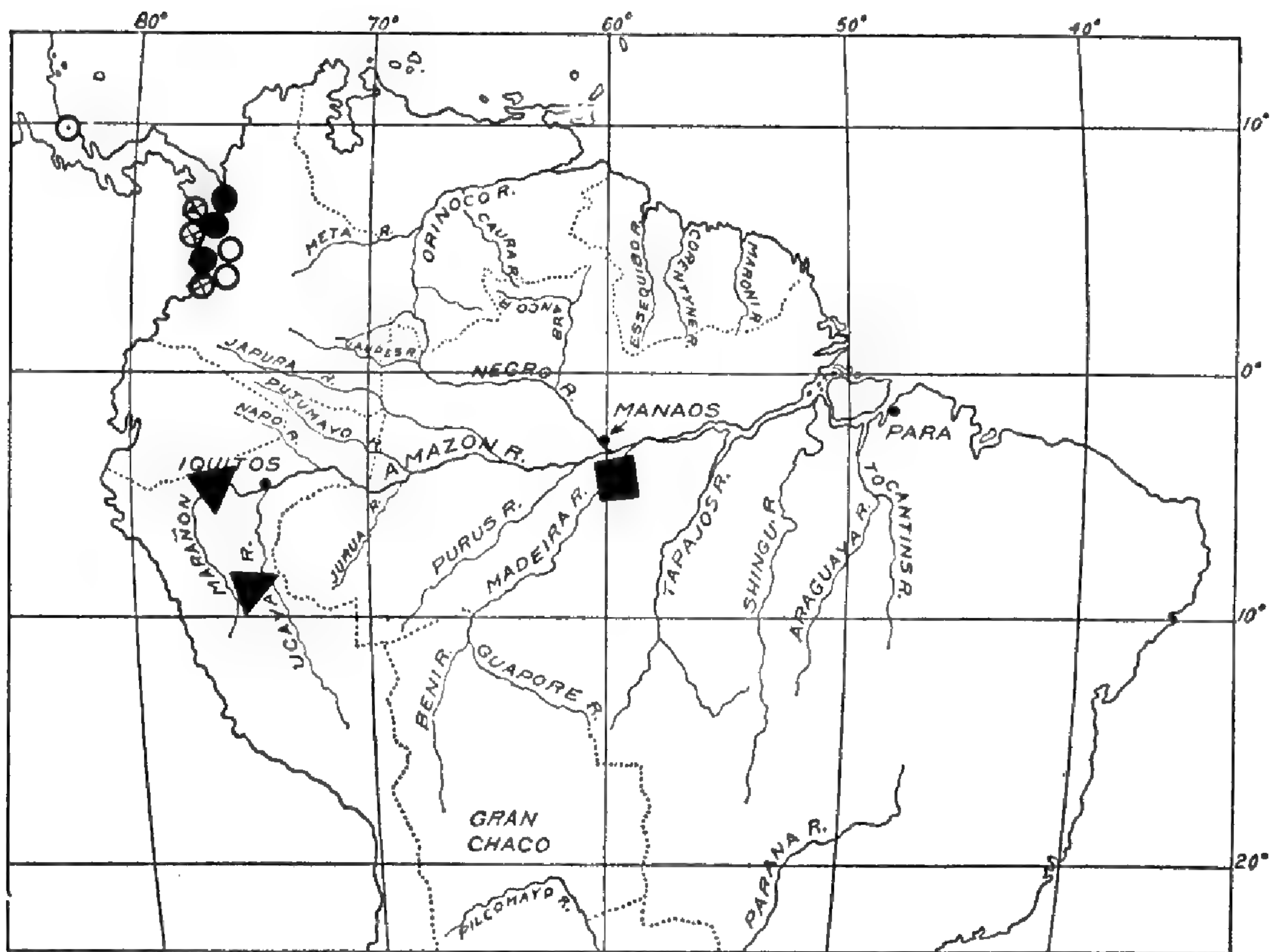
TRINIDAD: Royal Botanic Gardens, Port-of-Spain, *L. H. Bailey*, s.n. (BH). Ibidem; small tree, flowers orange colour, 8 IX 1918 (originally from Guatemala), *Broadway* 8935 (BM, BR, MO, S). Ibidem; tree 8 m., flowers orange yellow, 10 VII 1953, *R. E. D. Baker* s.n. (TRIN). Government House Gardens, 12 III 1929, *Williams* 12121 (TRIN). St. Augustine, Imperial College of Tropical Agriculture; tree 3–4 m. alt., lower branches horizontal, upper ones ascending, bark granulose, lenticellate, more or less cleft, yellowish brown, abundant, hanging, very rugose dried fruits, 1 IX 1961, *Cuatrecasas & Cope* 25789 (US). Ibidem; tree about 8 m. (9 years old), trunk 20 cm. in diam. at base, primary branches ternate from near the base, leaves thin-coriaceous, yellowish green, shining above, greenish cinereous beneath, 1 IX 1961, *Cuatrecasas & Cope* 27591 (US).

11. *Theobroma cirmolinae* Cuatr.

FIGURES 3, 4, 30, 32, 34, 36, 37; MAP 9; PLATE 7
Theobroma cirmolinae Cuatr. Notas Fl. Colomb. VI: 5, fig. 1–5. 1944;
 Rev. Acad. Colomb. Cienc. 6:32, fig. 1–5. 1944; Llano (1947) 34,
 pl. 14; Baker, Cope & al. (1954) 13, fig. 22; León (1960) 320, 317, fig.

TYPE.—El Valle, Colombia, *Cuatrecasas* 14897

Medium-sized or large tree up to 20 m. high; growth pseudoapical; trunk up to 40 cm. in diameter, branched in the upper third, the bark dark grayish, somewhat rimose-scaly, under the periderm brown or



MAP 9.—Geographical distribution of *Theobroma stipulatum* ●, *T. cirmoliniae* ○, *T. chocoense* ⊕, *T. mammosum* ⊙, *T. sinuosum* ▲, and *T. canumanense* ■.

rufous, the wood ochraceous, the hardwood ochraceous reddish, very hard; branches gray or brownish gray, the primary ternate, the terminal leafy branchlets tawny or ferruginous, appressed stellate-tomentose; gum resin flowing easily from bark and wood; stipules large, persistent, subcoriaceous, oblong-lanceolate, subacute, ochraceous-tomentose, 12–22 mm. long, 3–5 mm. broad at base.

Leaves of the young branchlets (smaller than in adult) thin-chartaceous, green-ochraceous with scattered stellate hairs above, green ochraceous or grayish green, appressed stellate-tomentose beneath; adult leaves large, thick-coriaceous, rigid, shortly petiolate; petioles very strong, thick, subterete, appressed ochraceous-tomentose, 1–2 cm. long, 6–8 mm. broad; blades oblong-elliptic or ovate-elliptic, slightly asymmetrical, rounded, cordate, or sharply emarginate at base, little attenuate, rounded or very obtuse and shortly acuminate at apex, entire or very slightly sinuate and flat at margin, 26–54 cm. long, 14–30 cm. broad, ochraceous green above, pale brown when dry, apparently glabrous but with scattered, appressed stellate hairs, these more copious on the main nerves, the costa and the secondary nerves filiform and depressed, the minor venation less noticeable, velvety-tomentose beneath, the surface rosy-glaucous, the veins somewhat more ferruginous or rufescent, the costa very thick and prominent, the 12–14 secondary nerves on each side very

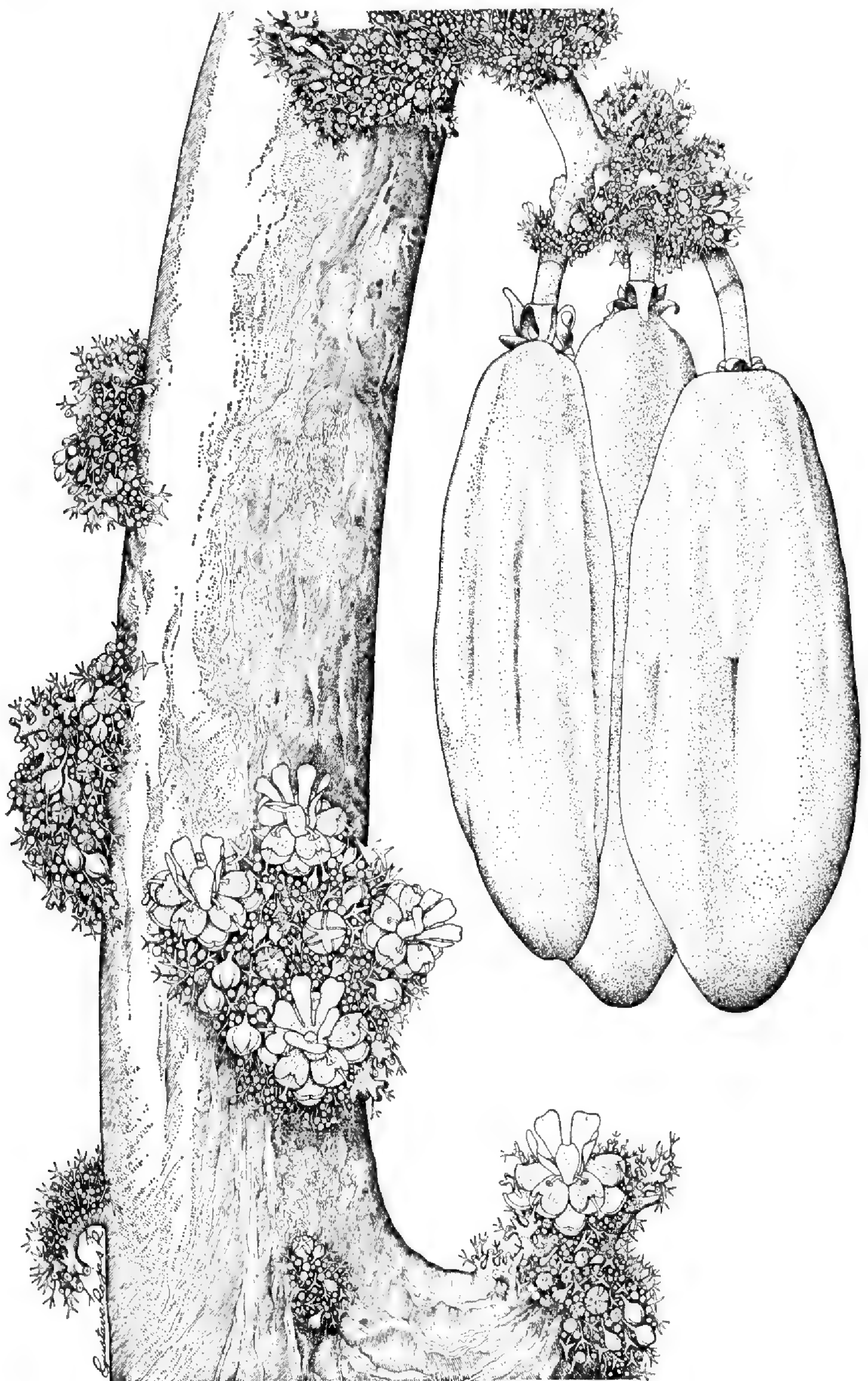


FIGURE 34.—*Theobroma cirmolinae*, flowering and fruiting trunk, $\times \frac{1}{4}$.

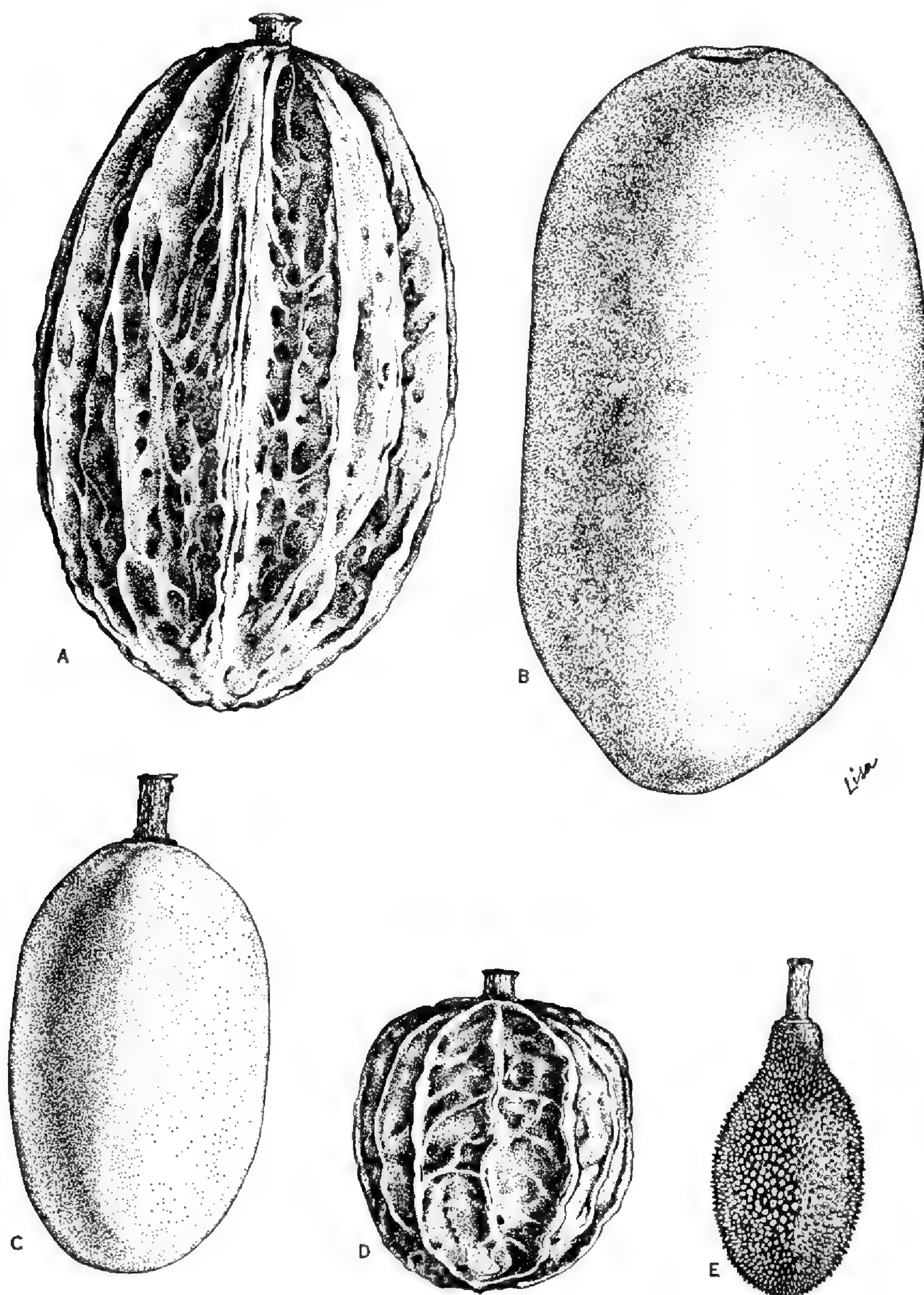


FIGURE 35.—Fruits of *Theobroma*, $\times \frac{1}{2}$: A, *bicolor* (Llano s.n.); B, *stipulatum* (Cuatr. 21339); C, *subincanum* (Little 9544); D, *microcarpum* (Archer 1551); E, *obovatum* (Klug 2983).

prominent, subspreading, near the margin arched, decurrent, anastomosing, the transverse tertiary nerves prominent, those of the fourth rank also prominent, reticulate-anastomosing, the lesser veins forming a minute, prominulous reticulum, the minor reticulum and areoles covered by a dense tomentum of intricate, white, sericeous, minute

stellate hairs, the major nerves with only scattered minute, slightly larger hairs and abundant, minute reddish, callose warts; base of lamina 7-nerved, the 4 lower nerves small, of lower degree.

Fertile branches perennial on main trunk and big branches, short, ligneous, tuberculate, prolific in flowering, the short, intricate, cin-

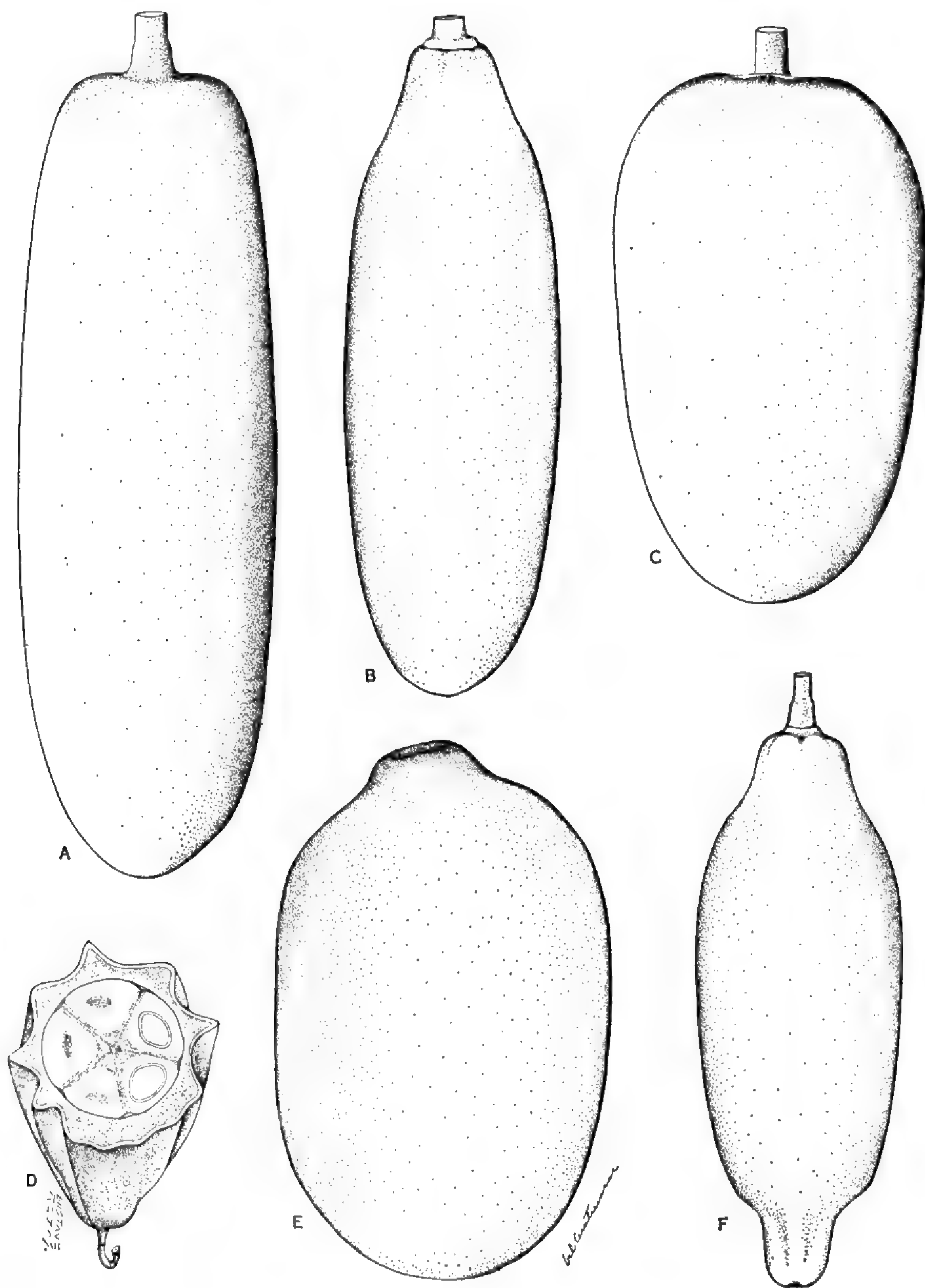


FIGURE 36.—Fruits of *Theobroma*, $\times \frac{1}{3}$: A, *simiarum* (Cuatr. 26515A); B, *simiarum* (Cuatr. 26536); C, *chocoense* (Patiño 115); D, *cirmolinae* (Cuatr. 15336); E, *grandiflorum* (Cuatr. 25780T); F, *mammosum* (Cuatr. 26535).

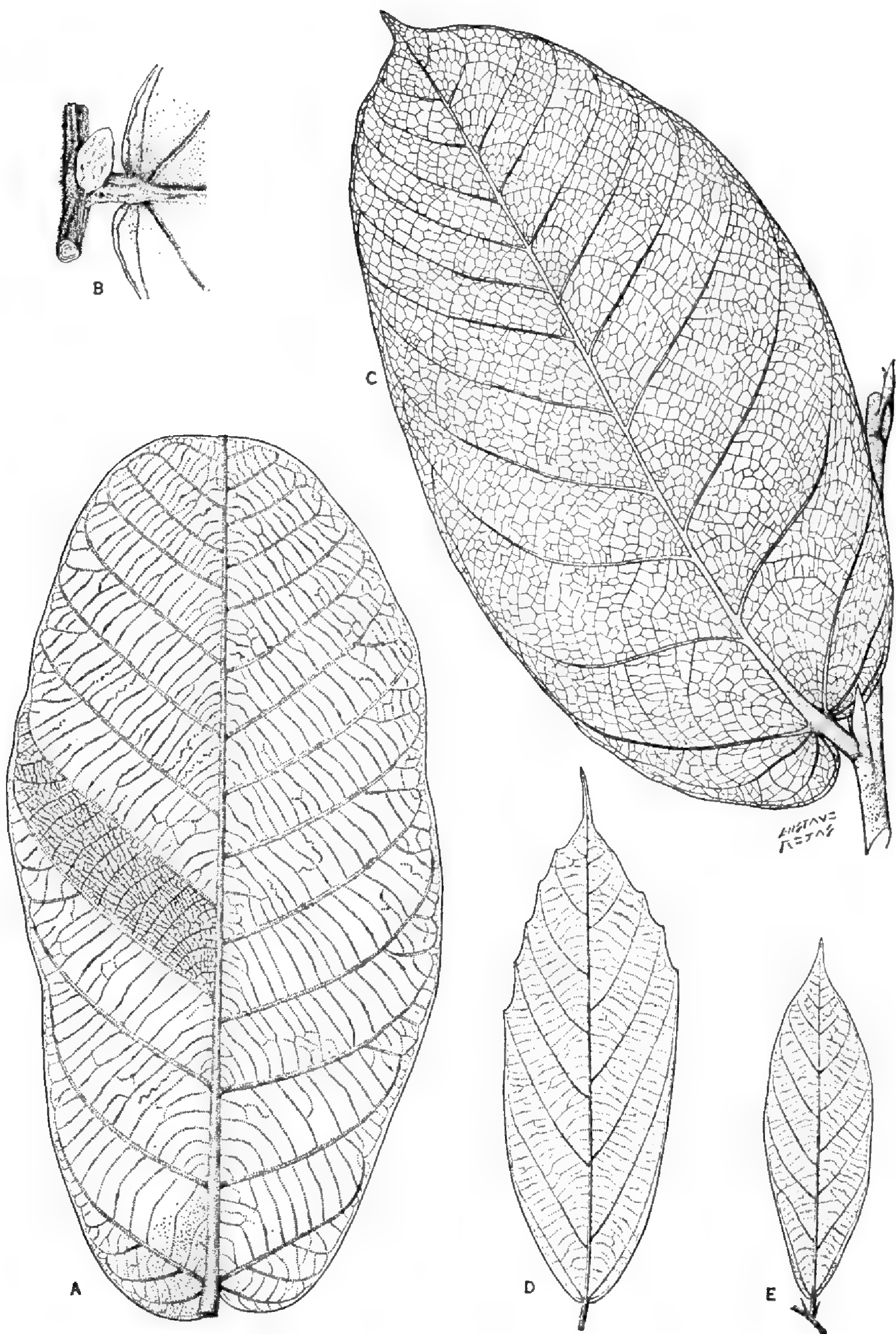


FIGURE 37.—Leaves of *Theobroma*: A, *stipulatum* (Cuatr. 21339); B, *stipulatum*, stipules and base of leaf beneath (21339); C, *cirmolinae* (Cuatr. 15336); D, *angustifolium* (Allen 6259); E, *angustifolium* (Stand. 22317), showing the stipules. All leaves $\times \frac{1}{3}$; B, $\times \frac{3}{8}$.

cinnate branches forming cushions up to 12 cm. broad on the trunk; sympodial branchlets angulate, ramose, bracteolate, forming crowded panicles up to 8 cm. long, appressed stellate-tomentose or glabrate when old; bracts 1.5–3 mm. long, 1.5–2.5 mm. broad, subcoriaceous, persistent, subamplectant, triangular-ovate, tomentose; peduncles elongate in anthesis, erect, rather thin, ferruginous tomentose, 5–8 mm. long, 3-bracteolate at apex; bracteoles linear, subacute, 3–6 mm. long, 1–1.5 mm. wide; pedicels in anthesis 15–20 mm. long, thin, erect, tomentose, ebracteate; buds globose, with 5 commissural ribs, densely ferruginous tomentose.

Sepals thick, carnose, ovate-triangular, acute, united in the lower third or fourth, soon umbilicate-reflexed, with the five free lobes spreading, 10–15 mm. long, 6–7 mm. broad, pale yellow inside, glabrous, except for the base, with minute, oblong, glandular hairs at their insertion, yellowish, thick-tomentose outside with ochraceous or tawny stellate hairs, the margin minutely cinereous-tomentose.

Petal-hoods yellow, thick-membranaceous, elliptic-obovate, rounded-cucullate at apex, glabrous, with 7 prominent nerves inside, 6–7 mm. long, 4–5 mm. broad; petal-laminae thick, carnose, glabrous, subtriangular-spatulate, slightly 3-undulate or emarginate at apex, about 3.5 mm. long, 2.2 mm. broad, tapering to a pedicel at base; pedicel about 4 mm. long, 0.6 mm. wide, bidentate at the joint.

Androecium tube thick, 2–2.2 mm. high; staminodes laminar, rather thick, oblong-spatulate, slightly broadened towards the end, retuse at apex, erect, glabrous, sulphur yellow, often somewhat reddish near the base, 10–11 mm. long, 4–5 mm. broad, at base 1.5 mm. wide; filaments robust, glabrous, 2.2–3 mm. long, shortly 3-furcate, 3-antheriferous, rarely 4-furcate, 4-antheriferous; ovary ovoid, 1.6–2 mm. long, 1.8 mm. broad, 5-costate, tomentose; styles 2 mm. long, connivent, free up to near the base.

Fruiting peduncle robust, 3–4 cm. long, 8–10 mm. thick, articulate; young fruits large, fusiform, prismatic with 5 obtuse, prominent ribs corresponding to the loculi and 5 others, more or less marked, alternate commissural ones, the base umbilicate, the apex attenuate and obtuse; ripe fruit 25–35 cm. long, 10–12 cm. wide, ellipsoid-oblong or obovoid-oblong, very little narrowed to the umbilicate base, attenuate to the obtuse apex, the surface obtusely pentagonal, with rounded ridges, brown or ferruginous, stellate-tomentose; pericarp about 1–1.5 cm. thick; epicarp 2 mm. thick, very hard, ligneous, the mesocarp and endocarp carnose, becoming hard and coriaceous when dry; covering of the seeds fibrous, pulpy, yellowish white and flavorful; seeds striped from the more or less compressed pulp, ovoid, the testa brown, the outer tegument light brown, the inner one dark brown, the cotyle-

dons reddish, 20–24 mm. long, 15–19 mm. broad, and 9–16 mm. thick; germination hypogeous.

COMMON NAMES.—Bacao, cacao de monte, cacao indio.

USES.—No special uses known besides occasional preparation of chocolate by the natives. This species is the one which grows at the highest altitudes; it should be tried as a grafting base, especially in the coldest zone of cacao production.

DISTRIBUTION.—Only known from the Pacific slopes of the Andes in Colombia in the Department of El Valle, between 800 and 1300 meters altitude.

COLOMBIA: EL VALLE: Western slope of western Cordillera, valley of Río Digua, Piedra de Moler, rain forests, 900–1180 m. alt.; tree 20 m., trunk 40 cm. in diam., adult leaves thick-coriaceous, green above, yellowish green beneath, sepals ferruginous-green, petals yellow, staminodes bright yellow, their bases reddish, bark and central wood with resine, “bacao,” 19 VIII 1943, *Cuatrecasas* 14897 (holotype VALLE; isotypes, F, Y). Valley of Río Digua, La Elsa, forests 1000–1200 m. alt.; tree 12 m., branched in the upper part, bark dark gray, almost smooth, flowers yellow, 9 XI 1943, *Cuatrecasas* 15336 (F, VALLE, Y, paratypes). La Elsa, about 800 m. alt.; tree 12–15 m., 30–35 cm. in diam. at base, jorquettes arising symmetrically, flowers (yellow) and fruit on trunk and main branches, mature fruiting peduncle 4 cm. long, 1 cm. thick, pod 26–28 x 10–11 cm., bluntly ridged, 23 VI 1953, *Holliday* 140 (COL, TRIN, US). La Elsa; tree 9–12 m., 30 cm. in diam. at base, jorquettes arising symmetrically, flowers yellow, fruit on trunk and main branches, 23 VI 1953, *Holliday* 139 (TRIN, US). Hoya del Río Sanquinín, left side, La Laguna, forests 1250–1400 m. alt.; tree 20 m. alt., yellow flowers, fruits large, brown tomentose, “cacao indio,” 20 XII 1943, *Cuatrecasas* 15700 (F, VALLE, Y).

12. *Theobroma stipulatum* Cuatr.

FIGURES 30, 32, 35, 37; MAP 9

Theobroma stipulatum Cuatr. Fieldiana Bot. 27(1):84, fig.7. 1950; Baker, Cope, et al. (1954) 14, line 15 (as *Theobroma* sp.); León (1960) 322, 315, fig.

TYPE.—*Cuatrecasas* 21339, Colombia, Chocó.

Large tree to about 30 m. high; growth pseudoapical; trunk about 45 cm. in diameter, somewhat triangular at base, the bark rugose, granulate, reddish brown, the wood dark ochraceous, hard; branches grayish, rugose-squamulose, glabrate, the primary ternate; terminal branchlets pale ferruginous tomentose, densely covered by stellate or fasciculate hairs; stipules coriaceous, densely tomentose, pale ferruginous, ovate or ovate-oblong, obtuse, persistent, 8–12 mm. long, 5–9 mm. broad, the terminal up to 25 x 11 mm.

Leaves large, strongly coriaceous; petioles robust, very thick, short, densely ferruginous tomentose, 5–10 mm. long; blades ovate-elliptic or elliptic, more or less oblong, rounded, truncate or obtuse at apex, the usually slightly asymmetrical base emarginate-cordate, entire or slightly sinuate and flat at margin, 23–45 cm. long, 11–17 cm. broad, green above, when dry brown or pale brown, slightly rugose or

almost smooth, with scattered, minute, stellate hairs, the costa and secondary nerves linear, tomentose, depressed, greenish ochraceous beneath or when dry ochraceous brown or pale brownish, tomentose, covered with minute, whitish, intricate, stellate hairs, and other mediocre, thicker, ferruginous, stellate hairs copiously covering the veins, the costa very robust and prominent, the secondary nerves about 12 on each side, very prominent, subascending, near the margin curved, decurrent, and anastomosing, the transverse tertiary nerves prominent, parallel, 5–15 mm. distant from each other, the minor veins prominently reticulate.

Inflorescences cauline, on trunk or main branches, the fertile branches perennial originating from tubercles; ligneous branches short, tortuous, intricate, furcate-ramose (dichasial and cincinnate), bracteate, tomentose, up to 1–3 cm. long; bracts ovate, subcoriaceous, tomentulose, minute; peduncles solitary, 5–12 mm. long, thin, stellate-tomentose, 3 bracteolate and 1-flowered at apex; bracteoles linear, acute, 2–3 mm. long; pedicels erect, thin, densely tomentose, 10–22 mm. long; buds globose, 10–14 mm. in diameter, sublanate-tomentose; sepals thick, ovate-triangular, glabrous and ochraceous inside, except for the minute, thick, oblong, glandular hairs at base, densely stellate-tomentose or sublanate outside, 10–15 mm. long, united in the lower third, reflexed at anthesis, umbilicate at base; petals yellow, glabrous, the hoods obovate elliptic, 7-nerved-sulcate, involute at margin, round-cucullate at apex, about 5 mm. long and 3–4 mm. broad; petal-laminae yellow, thick, 3–3.5 mm. long, ca. 3–3.5 mm. broad, suborbicular or subspatulate, slightly retuse at apex, attenuate into a narrowly linear pedicel at base, this 3.5–4 mm. long.

Androecium tube 1.5–2 mm. long, glabrous; staminodes petaloid, yellow, thick, glabrous obovate-oblong, subspatulate, rounded at apex 1-toothed on each side, 10–11 mm. long, 4.5–5 mm. broad, at base 1.5 mm. broad; filaments rather thick, glabrous, 1.8–2 mm. long, curved, shortly 3-furcate, 3-antheriferous; anther lobes ellipsoid; ovary ovoid-oblong, 5-furrowed, densely tomentose-hirsute, about 2 mm. high; styles filiform, glabrous, coherent, about 2 mm. long.

Fruit 17–22 cm. long, 9–11 cm. broad, ovoid-ellipsoid or ellipsoid and oblong, rounded at base, slightly attenuate, obtuse or rounded at apex; pericarp hard-coriaceous, rigid, smooth, appressed brown tomentose, the epicarp woody, about 1.5 mm. thick, the mesocarp and endocarp carnose, creamy, about 1 cm. thick; seeds compressed about 20–55, surrounded with pale, yellowish white, soft, scented pulp, more or less amygdaliform, 20–25 mm. long, 18–21 mm. wide, and 7–10 mm. thick, the testa subcoriaceous about 0.5 mm. thick; cotyledons white; germination hypogeous; fruiting peduncles robust, 1–3 cm. long, about 1 cm. thick.

COMMON NAMES.—Chocolate de monte, cacao de monte.

USES.—The seeds are said to yield a good chocolate but they are only occasionally used by the natives.

DISTRIBUTION.—Restricted to the rain-forested basins of the rivers San Juan and Atrato (Chocó region) and perhaps Río Sequión (Nariño) in western Colombia, where it is of rare occurrence.

COLOMBIA: ANTIOQUIA: Villa Arteaga, about 100 m. alt.; tree 12 m., 20 cm., diameter base, flowers borne on trunk and main branches, pedicel from base to bracts 1.6 cm., from bracts to flower 2.2 cm., bracts 3, one usually larger, abscission layer near bracts, sepals joined about $\frac{1}{3}$ way from base, reflexed when flower opens, all parts of flower yellow, 7 ridges on inside of petal, staminodes spatulate, 14 mm. long, 6 mm. wide, 22 VII 1953 *Holliday & Bartley T/165* (TRIN, US). Ibidem, and same tree; *Cope Ant.* 2 (specimens lost), field annotations by Cope: "A branched tree, showing the branching of the *subincanum* group, new growth from above jorquette; 3 branches." "Interior parts of bud examined were creamy white; sepals reflexed in opened flower, 7 mm. long x 4 mm. wide, elliptic, pointed, apparently rather soft and spongy, truncate margins, free almost to base, inner surface glabrous; petals 5, free, with cup-shaped base and ligule, base 4 x 4 mm., ligule and strap 5 mm. long, expanded portion spatula-shaped, staminodes 5, reflexed, oblanceolate, 10 mm. x 3 mm., fruit somewhat ovate in outline, in cross section, slightly flattened on 5 side, no ridges or furrows, densely covered with medium brown, stellate hairs, which impart a mealiness to surface, 18 cm. long x 10 cm. diameter, wall with woody outer layer about 1.5 mm. thick, inner surface very soft, creamy, about 1 cm. thick, 55 seeds embedded in soft, cream-colored tissue, beans flattened, up to 1 cm. thick, somewhat triangular in outline, up to 25 mm. long x 21 mm. wide, testa chocolate brown in color, about 0.5 mm. thick, rather leathery, cotyledons pure white, markedly convoluted, pulp has smell of green bananas."

CHOCÓ: Río San Juan, right margin of river on low hill near Palestina, about 30 m. altitude; tree 32 m. tall; trunk triangular at base, 45 cm. diam., branchless up to 25 m. height, bark rugate-granulate reddish brown, wood rather dark ochraceous, leaves coriaceous, rigid, green above, ochraceous green beneath, when very young light yellowish green above, young branchlets and stipules pale ferruginous, fruits oblong-ellipsoid or oblong-subovoid, obtuse, dark brown tomentose, 17–22 cm. long by 9–10 cm. broad, pericarp rigid woody, "chocolate de monte," 28 V 1946, *Cuatrecasas* 21339 (holotype, F; isotypes, US, VALLE, Y). Río Atrato, Lloró; young tree 3 m., sterile, jorquette of three branches, 4 VIII 1953, *Holliday & Bartley* 175 (TRIN, US).

NARIÑO: Iscuandé, Río Sequión, 100 m. alt.; tree 18 m., bark reddish and smooth, wood cream colored, "chocolate," 23 XI 55, *Romero Castañeda* 5500 (COL). (A sterile specimen, the identification is doubtful; flowers and fruits necessary.)

13. *Theobroma chocoense* Cuatr., sp. nov. FIGURES 3, 31, 36, 38; MAP 9

Arbor 8–15 m., trunco erecto pseudoapicale crescente, cortice sublaevi, ramis ternatis robustis patulis superioribus ascendentibus ramulis alternis juvenilibus dense crasseque lanuginoso-tomentosis viridi-ochraceis vel viridi-ferrugineis, pilis stellatis intricatis mediocribus ochraceis densis et pilis fasciculatis longioribus pallidis sparsis tectis, denique glabratis brunneis nitidis angulosis cicatricosis; stipulae coriaceae persistentes petiolis longiores ovatae obtusiusculae longi-

tudinaliter striato-nervatae primum ochraceo-tomentosae, pilis ferrugineis mediocribus stellatis, deinde cinereae, pilis stellatis minutis albidis adpressis munitae, intus glabrae 12–22 mm. longae, 10–15 mm. latae, in ramis valde juvenilibus ovato-lanceolatae 2–25 mm. longae, 8–9 mm. latae.

Folia alterna rigide coriacea; petiolus brevis crassus robustus viridi-ochraceus vel viridi-ferrugineus dense lanuginoso-tomentosus, pilis mediocribus stellatis densis et pilis fasciculatis longissimis (ad 2 mm. longis) pallidis sparsis, 7–14 mm. longus, 8–10 mm. crassus; lamina oblongo-elliptica vel subovato-elliptica, integra vel levissime undulata, basi ampla leviter attenuata subsymmetrica rotundata cordato-emarginata, apicem versus paulo attenuata apice obtusa subite acuteque acuminata 18–42 cm. longa, 9–20 cm. lata, acumine 1–1.5 cm. longo, supra juventute ochraceo-stellato-tomentosa deinde glabra vel sparsissimis pilis stellatis mediocribus munita, plus minusve venoso-rugosa, nervis secundariis filiformibus impressis, nervulis venulisque plus minusve impressis, superficie lutescenti-viridi in sicco brunnescente, subtus valde nervosa viridi-cinerea in sicco ochraceo-ferruginea, costa crassa valde eminente, nervis secundariis valde prominentibus 12 vel 13 utroque latere paulo ascendentibus ad marginem arcuatis, nervis tertiariis transversis parallelis prominentibus 3–10 mm. inter se distantibus nervulis minoribus venulisque bene prominentibus reticulatis, indumento heterotricho-tomentoso, superficie alveolorum venulisque reticuli pilis-stellatis minutissimis tenuibus albidis intricatis dense tectis, nervis alteris copiosis punctis callosis rubris et copiosis, pilis stellatis majoribus ferrugineis radiis patulis munitis, in foliis vetustis nervis majoribus saepe glabratis, in prole foliis tenuioribus subtus albo-cinereis, pilis minutissimis stellatis albis dense tecta, in nervulis sparsis in petiolo costa nervisque principalibus densis pilis stellatis ochraceis radiis patulis gracilibus 1–1.5 mm. longis basi calloso-rubescence praedita.

Folia prolis orthotropae tenuia petiolata late ovata vel rhomboideo-ovata sursum crenato-dentata apice acuminata, circa 8 nervis secundariis utroque latere; lamina 12–20 cm. longa, 8.5–12 cm. lata, petiolo 3.5–4 cm. longo, vel latiore; stipulae anguste lanceolatae.

Inflorescentiae in trunco et in ramis majoribus copiosae, tuberculis lignosis persistentibus orientes, ramulis brevissimis cymosis tomentosis densos glomerulos floriferos formantibus; bracteae lineares circa 5 mm. longae ferrugineo-tomentosae; pedunculi ad 1 cm. longi tomentosi apice 3-bracteolati; bracteolae anguste lineares 2–2.5 mm. longae tomentellae; pedicelli 9–14 mm. longi erecti mediocres stellato-tomentosi viridi-ochracei; alabastra ellipsoideo-(globoso)-depressa 9–10 mm. lata, 7–8 mm. longa, in commissuris 5-costata, minute ochraceo-tomentosa; calyx basi cupularis, intus basi ad marginem insertionis

annulo pilis densis crassis glandulosis praeditus, in anthesin reflexus; sepala 5 crassiuscula ovato-acuta, 10–11 mm. longa, circa 7 mm. lata, basi 2.5–3 mm. longe in tubum coalita, extus minute ochraceo-stellato-tomentosa, margine minutissime albo-tomentosa, intus glabra superne parce pilosula excepta.

Petala glabra, cucullo crassiusculo pallido obovato-suborbiculato circa 6 mm. longo et lato, basi amplo apice subrotundato depresso apiculo bidenticulato, venulis 7 extus paulo conspicuis intus prominentibus; lamina crassa rigida rubra obovato-deltaidea apice subtruncata, 5–6 mm. longa, 5–6.5 mm. lata, basi attenuata et cum pediculo circa 3.5 mm. longo articulata.

Androecii tubus crassiusculus glaber circa 1.5 mm. altus; staminodia petaloidea crassiuscula glabra in anthesin erecta obovato-oblonga apice rotundata margine integra basim versus gradatim attenuata, 13–15 mm. longa, 5–7 mm. lata, basi 3–3.2 mm. lata; stamina filamentis crassiusculis circa 2 mm. longis recurvatis glabris, antheris 3, lobis bilocularibus loculis ellipsoideis circa 0.6 mm. longis; ovarium globosum 2.5 mm. diam. dense hirsuto-tomentosum; styli circa 2 mm. longi.

Fructus laevis ellipsoideo-ovoideus basi late rotundatus apice paulo attenuatus obtusus, 19–20 cm. longus, 10–11.5 cm. latus, pericarpio crasso duro, extus crasse brunneo-tomentosus, epicarpio circa 2 mm. crasso lignoso; semina ovoidea vel triangulari-ovoidea compressa, 20–23 mm. longa, 16–18 mm. lata, 11–12 mm. crassa.

Type in the U.S. National Herbarium, No. 2402158, collected on the grounds of the Experimental Station "Agroforestal del Calima," Bajo Río Calima, at about 35 m. altitude, in the Department El Valle, Colombia, September 25, 1961, by J. Cuatrecasas and L. Willard (No. 26074). Flowers from the same tree collected by H. Guerrero A. (No. 26074) December, 1961. Paratype collected at the same place with a dry mature fruit by V. M. Patiño (No. 115).

COMMON NAMES.—Cacao de monte, cacao grande de monte, bacao de monte.

DISTRIBUTION.—Restricted to the Chocó region, in the heavy forested valleys of the rivers San Juan and Atrato in western Colombia. The records of *T. simiarum* from the Calima River by Baker, Cope & al. (1954, 14) refer to this species.

Theobroma chocoense is closely related to *T. simiarum*, from which it differs in its broadly ovoid or ellipsoid pods, in its elliptic or ovate leaves (instead obovate), in the indument of the lower side of the leaves, which is composed of two kinds of hairs (minute, entangled, white, stellate hairs covering the surface and larger ones with long, spreading rays on the nerves), by the short, ovate, obtuse stipules, and shorter bracteoles. All these features indicate that Chocoan

species is distinct from the Costa Rican species. Although the fruit of *T. chocoense* is very similar to that of *T. stipulatum*, the red color of the flower and the different indument of the leaves readily distinguish these two species.

COLOMBIA: EL VALLE: Baja Calima (Chocó region), Río Calima, Estación Agroforestal del Calima, 30–40 m. alt.; tree about 8 m. high, with apical growing trunk almost smooth with few fertile tubercles, primary branches ternate, abundantly inflorescence-tuberculate, leaves rigid, medium yellowish green above, cinereous green beneath, "cacao de monte," 25 IX 1961, *J. Cuatrecasas & L. Willard* 26074 (holotype, US; isotype, COL). Ibidem; flowers purple red, XII 1961, *Humberto Guerrero* 26074 (US). Ibidem; small tree (about 10 m.) on the edge of the small creek behind the Palmetum, dry fruit 19 x 11.5 cm., I 1953, *V. M. Patiño* 115. Ibidem; tree 12–15 m. in forest, fruit 16 x 11 and 20 x 10 cm., quite smooth, no flowers, 29 VI 1953, *Holliday* 144 (TRIN, US). Río Calima, Caño la Brea; young tree 2 m., in forest, sterile, 29 VI 1953, *Holliday* 143 (TRIN, US).

Chocó: Río San Juan, in front of Palestina, Quebrada de la Sierpe, 0–40 m. alt.; tree about 14 m. high, trunk 30 cm. diam., leaves rigid, rugose, coriaceous, deep green above, cinereous green beneath, strongly nerved, fruit ellipsoid, smooth, velvety tomentose, 20 cm. long, 10 cm. wide, the seeds acid, "bacao de monte," 13 III 1944, *J. Cuatrecasas* 16896 (F, VALLE, US).

13a. *Theobroma chocoense* var. *bullatum* Cuatr., var. nov.

A var. *chocoensi* foliis rugosis reticulato-bullatis differt. Lamina rigida elliptico-oblonga vel paulo obovato-oblonga, magna, usque ad 50 x 21 cm., basi rotundata, apice rotundata breviter subiteque cuspidata, juvenilis basim versus plus minusve attenuata apice magis angustato-acuminata; cucullum petalorum 5–6 mm. longum, 3–4 mm. latum, pediculo 3.5–4.5 mm. longo; lamina triangulari-spathulata, 2.5–4 mm. longa, 2.5–3 mm. lata; staminodia obovato-oblonga apice rotundata, circa 10 mm. longa, 4 mm. lata, basi 1.5 mm. lata; sepala extus tomentosa intus glabra, circa 12 mm. longa, 5 mm. lata, 3 mm. basi coalita.

Type in the U.S. National Herbarium, No. 2404636, collected in Quebrada Juan María, a small tributary of Río Juradó, at about 500 m. from its mouth, in the Municipality of Nuquí, Department of Chocó, Colombia, at 50–100 m. altitude, on a hill in a region having a dry season of about 4 months, 15 II 1955, *V. M. Patiño* 171.

Although at first sight the leaves of this variety look very different from typical *T. chocoense*, no other differences can be found on the basis of the available material. According to fragmentary data it seems that the fruit of the Juradó specimens are identical with those of *T. chocoense*. The leaves are strongly nerved, reticulate and rugose-bullate, but some specimens of typical *T. chocoense* also show rugosity in the leaves. *V. M. Patiño* writes about his specimens: "Tree 12–14 m. alt., the trunk straight, triangular on the lower half, with sides

about 30 cm. broad, tubercular, floral cushions copious on the whole trunk; the specimens are scattered; no other trees were seen in the vicinity; the "cuzumbies" like its fruits very much, for which reason it is difficult to find them unbroken; branches few, terminal; leaves 40–50 x 16–21 cm., petiole 1–1.5 cm., 6–11 mm. thick; leaves of very young specimens dentate in their upper half; fruits on trunk and branches; the 2 flowers collected were dry but a Choko Indian told that its natural color is red and that the seeds are purplish; the Choko name for the species is "cumajó" or "judromajó."

To this variety belong the sterile specimens from Río Atrato referred to by Baker, Cope and al. in their Report, page 14 as "*Theobroma* sp. (possibly new)." Additional flowering and fruiting collections of this plant are needed to complete our knowledge and to determine better its taxonomic rank.

COMMON NAMES.—Chocolate de monte, bacaíto de monte, cumajó (*Chokó*), judromajó (*Chokó*), according to Victor M. Patiño notes.

USES.—The pulp is acid and of pleasant taste, for which reason it is sought by animals and also by the Indians.

DISTRIBUTION.—Río Atrato and northwestern Pacific drainage, Chocó (Colombia).

COLOMBIA: Choco: Río Atrato, Lloró, about 50 m. alt.; tree 12 m., 4 VIII 1953 *Holliday & Bartley* T/176 (K, TRIN, US). Municipality Nuquí, Río Juradó, Quebrada Juan María, about 500 m. from mouth, 50–100 m. alt., 15 II 1955, *Patiño* 171 (US). Ibidem, seedling, *Patiño* 171A (US); first branches of a young plant, *Patiño* 171B (US).

14. *Theobroma simiarum* Donn. Smith. FIGURES 5, 6, 32, 36, 38, 40; MAP 8
Theobroma simiarum Donn. Smith in Pittier, Prim. Fl. Costar. 2: 52. 1898;
 Bot. Gaz. 25: 145. 1898; DeWildeman (1902) 97; Standley (1937) 689;
 Chevalier (1946) 282; Holdridge (1950a) 2; Allen (1956) 343; León (1960)
 322, 321, fig.

TYPE.—Turrialba, Costa Rica, *Tonduz* 8373 (= 7313 distributed J. Donnell Smith). Lectotype: US 1,382,332 [Photo F. M. 40723], US 471,873 [Photo F. M. 40722]. Syntypes: *Pittier & Tonduz* 3925, *Tonduz* 6852, *Cooper* 10244.

Medium to large tree up to 20 m. tall, with erect, thick trunk up to 60 cm. in diameter at the triangular base; growth pseudoapical; bark more or less rugose; branches spreading, the primary ternate, the upper ones ascending; young branchlets thick-tomentose, greenish ferruginous or brownish, covered by three kinds of hairs: 1) abundant minute squamose stellate hairs with thin rays, 2) mediocre stellate, longer hairs and 3) scattered large stellate or furcate hairs with very long white rays, when older glabrate, brownish or grayish; stipules persistent, longer than the petioles, subcoriaceous, firm, erect, lanceo-

late or linear, acute, 15–24 mm. long, 3–6 mm. broad, tomentose outside.

Leaves large, rigid, coriaceous; petiole robust, thick, somewhat striate, thick-tomentose-ferruginous, 5–12 mm. long, 6–10 mm. thick; blades obovate-oblong, rounded or very obtuse and abruptly cuspidate at apex, broad or slightly narrowed, rounded or slightly cordate and asymmetrical at base, entire or sinuate-dentate in the upper third, in very young plants obovate-rhomboid, long-acuminate, the upper half or third repand, acutely dentate, the adult 20–40 cm. long, 8–17 cm. broad, the acumen 0–1 cm. long, green above, when dry pale brown, smooth, glabrous or with scattered stellate hairs on the midrib, this and the secondary nerves filiform and depressed, the other veins usually obsolete, light green beneath, when dry cinereous or whitish but the nervation ferruginous, the costa thick, very prominent, the 9–11 secondary nerves on each side thick and prominent, spreading-ascending, the lower pair usually at a more acute angle, the transverse tertiary nerves prominent, separated 5–10 mm. from each other, the minor nerves and veins prominulous, reticulate; indument heterotrichous, the areolar surface and the small reticular veins covered by a dense tomentum of intricate, minute, white, stellate hairs, the thicker nerves with sparse mediocre, ferruginous, stellate hairs and reddish callous scars, the costa densely ferruginous by more or less copious mediocre hairs and other ochraceous, long ones; in seedlings the under leaf surface whitish, covered with a white tomentum of extremely minute, white, stellate hairs, and on the nerves sparse and on the costa dense ferruginous stellate hairs with long (1 mm.), thin, patulous rays and red, callous bases.

Inflorescences borne on tubercular protuberances on the trunk; cymose branches usually cincinnate, ligneous, very short, forming dense, many-flowered glomerules; branchlets up to 4 cm. long, tortuous, rugose, glabrate, bracteate, the bracts coriaceous, ovate, subacute or acuminate, tomentulose outside, 1–2 mm. long, 1–1.5 mm. broad, persistent; hornotinous branchlets short, crowded, ferruginous-tomentose, covered by fertile, tomentose, imbricate bracts; peduncles axillary, mediocre, densely stellate-pilose-tomentose, 5–15 mm. long, 3-bracteolate at apex, the bracteoles narrow-linear, tomentose outside, 3–7 mm. long; pedicels up to 15 mm. long; buds globose, densely tomentose, above almost 5-angulate; calyx cupular at center, subglabrous, with a ring of minute, thick, oblong, glandular hairs at base and with very thin hairs above inside, densely and thickly stellate-tomentose and ochraceous green or ferruginous outside, the sepals ovate-acute, about 10–12 mm. long, 6 mm. broad, united about 2 mm. at base, reflexed at anthesis; petals red, thick, glabrous; hood yellowish white, obovate-oblong, with 7 prominent nerves inside,

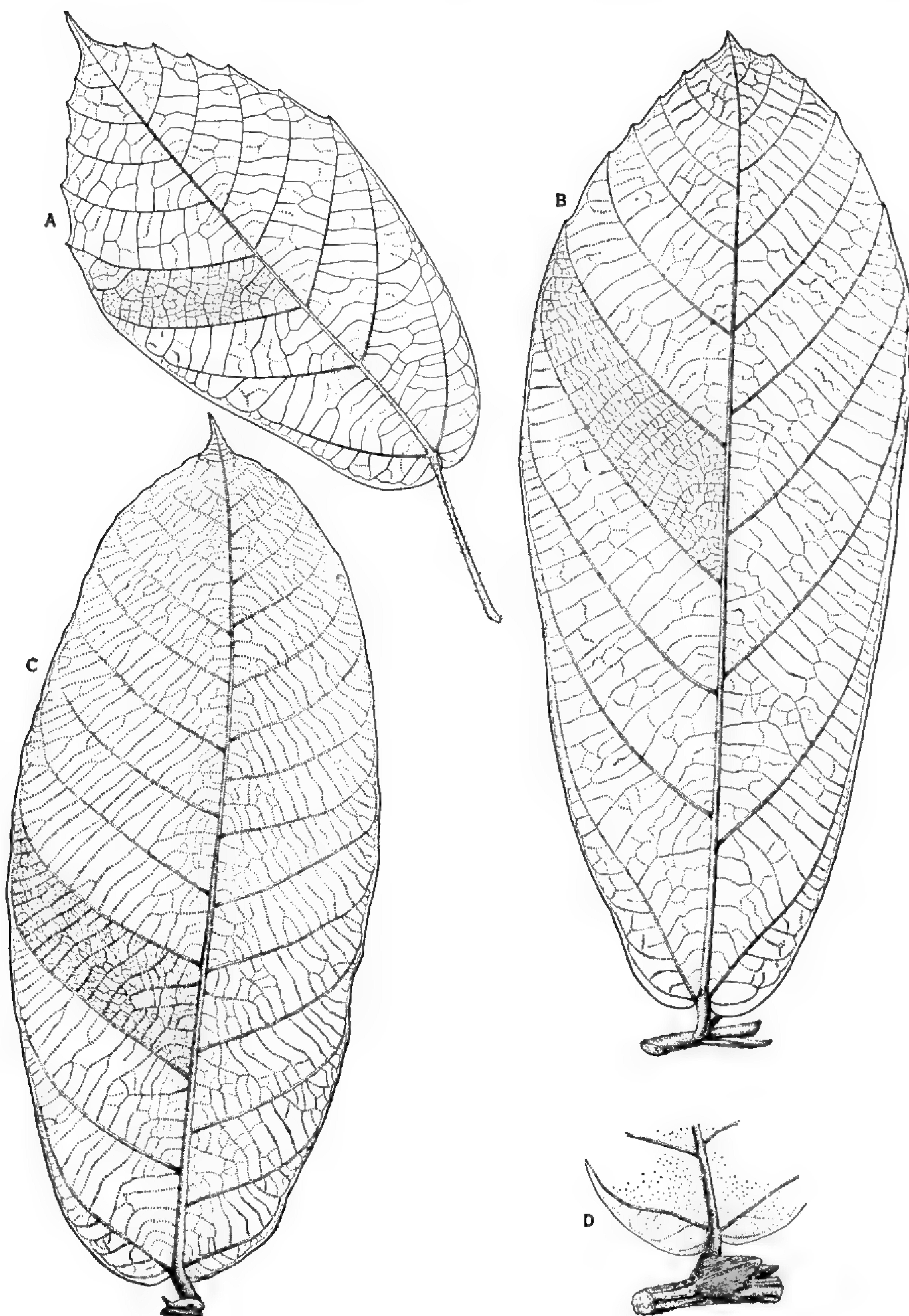


FIGURE 38.—Leaves of *Theobroma*: A, *simiarum*, from orthotropic stem (Stand. 37377); B, *simiarum*, from normal lateral branches (Cooper 10244); C, *chocoense* (Cuatr. 26074); D, leaf base and stipules of *T. chocoense* (Cuatr. 26074). All leaves $\times \frac{1}{3}$; D, $\times \frac{2}{3}$.

narrowed-unguiculate, and inside reddish at base, 6–8 mm. long, 4–5 mm. wide, rounded-cucullate, inflexed-apiculate at apex, the apiculum bifid, articulate to the pedicellate lamina; petal-lamina obtrapezoid, carnose, red, subtruncate at apex, cuneate at base, 3.5–4.6 mm. long, 3.5–5 mm. wide, reflexed in bud, erect in anthesis; pedicel linear, 4–5 mm. long, 1 mm. broad; androecium tube about 2 mm. long, rather thick, glabrous; staminodes petaloid red, glabrous, obovate-oblong, rounded at apex, slightly sinuate-dentate in the upper third or subentire, 11–13 mm. long, 5–7 mm. broad, 1–2 mm. wide at base, reflexed in bud, erect at anthesis; filaments rather thick, glabrous, curved, 2 mm. long, shortly 3-furcate, 3-antheriferous; anther lobes ellipsoid, 0.6–0.7 mm. long; ovary obovate, densely hirsute-tomentose, about 1.2 mm. high; styles about 1.2 mm. long, thin, acute, united at base.

Fruiting peduncle short, thick, usually 1–1.5 cm. long; fruit ellipsoid-oblong, smooth, truncate or very blunt, rarely narrowed at base, rounded, very obtuse or slightly attenuate at apex, 16–35 cm. long, 6–10 cm. broad, covered by dense and thick, ferruginous or brown tomentum; pericarp 11–15 mm. thick with: 1) epicarp woody, 1.5–2 mm. thick, with a tomentose epidermis, 2) mesocarp 5–10 mm. thick, firmly carnose, pale ochraceous whitish, and 3) endocarp 2–5 mm. thick, softer carnose; seeds 36–60, distributed in 5 more or less double rows, each one covered by a thick, fibrose, white or rosy-white, aromatic pulp irregularly ovoid, 20–21 mm. long, 18–17 mm. broad, and 13–15 mm. thick; cotyledons white; germination hypogeous.

COMMON NAMES.—Cacao de mico, cacao de mono, teta negra. Indian names: Kráaku (*Guatuso*), Nunísup (*Rama*), Uirub (*Bribri*), Dzug-mang-uá (*Brunka*), Ku-gín, Bik (*Térraba*), according to Standley, loc. cit., Uir-ub (*Bribri*) according Pittier.

USES.—The seeds are said to give a cacao of good quality. They are occasionally used.

DISTRIBUTION.—Limited to Costa Rica. Infrequently found in preserved or remnant forests in both Atlantic and Pacific lowlands, from sea level to 600 m., and exceptionally in higher altitudes up to 900 m.; recorded from the provinces of Limón, Heredia, Puntarenas, and Cartago. It may extend to Nicaragua and northern Panama, but no records from these two countries exist at present in herbaria.

In its natural habitat *T. simiarum* attains a considerable height and thickness. The trunk is erect and branchless up to several meters. The inflorescences may appear on the trunk but they are more abundant on the big branches. The fruit is very characteristic because of its terete, sausage shape. From the closely related Colombian species *T. stipulatum* and *T. chocoense* it can be distinguished by the elongate

shape of the pod; in the two other species the fruit is ovoid or broadly ellipsoid. From *T. stipulatum* it differs also by its red flowers, longer lanceolate stipules, longer bracteoles, and by the indument of the leaves. From *T. chocoense* it differs also by its narrower and longer stipules, the obovate form of the leaves, by the leaves having beneath usually three kinds of hairs, and by its longer bracteoles.

COSTA RICA: CARTAGO: Turrialba, grassland, 570–600 m. alt., XI 1893, *Tonduz* 8373 (distributed by Donn. Smith under number 7313) lectotype US; isoelectotypes BR, G, GH, K; Photos F. M. 30722, 40723, 40743. Turrialba, forest at margin of Río Reventazón, about 600 m. alt.; tall tree with unbranched trunk in the lower half, 60 cm. diam. near the subtriangular base, abundant tuberculate inflorescences on the upper part and big ternate branches, few sausage-shaped pods, 6 XI 1961, *J. Cuatrecasas & León* 26515A (US). Turrialba, Instituto Interamericano C.A., 600 m. alt.; flowers bright red, cult., 4 XI 61, *J. Cuatrecasas & J. León* 26515 (US). Turrialba, I.I.C.A., 600 m. alt., cult., 14 III 51, *J. León* 3189 (TURRI). Tuis, forests, 670 m. alt., “cacao de mico,” XI 1900, *Pittier* 14016 (*Donn. Smith* 7731) (GH, K, US). Tucurrique, grassland and forests around Las Vueltas, about 635 m. alt.; large tree, fruits brown, oval-elongated 30–40 cm. long, XI 1898, *Tonduz* 12822 (BM, G, LE, P, US), 18222 (M) [erroneous number].

LIMON: La Colombiana Farm of the United Fruit Company, about 70 m., wet forest; tree 60 feet or more tall with trunk 2 ft. thick, small crown, flowers bright red in bunches on trunk, fruit sausage-shaped, hairy, 1 foot long or more, said to be rare here, seeds give good cacao, 6, 7 III 1924, *Standley* 36822 (US). 28 miles on the railroad from Puerto Limón, towards Río Barbilla, in marginal forest, about 60 m. alt.; tall tree, flowers flame red, 12 V 1930, *Cufodontis* 599 (WU). Along Río Reventazón, below farmhouse Finca Castilla, 30 m. alt., in *Gynerium sagittatum* thickets, 27 VII 1936, *Dodge & Goerger* 9420 (MO). Palm swamp between Río Reventazón and Río Parismina, on Castilla Farm, 2 IV 1930, *Dodge & Nevermann* 7164 (MO). La Lola, farm of the I.I.C.A., about 40 m. alt., cult.; trees about 10 m. high, trunk 20–30 cm. diam., triangular at base, flowers scarlet, fruits oblong 15.5 x 7 cm., 18 x 8.7, 19.5 x 8.5, 22.7 x 7.7, 23.3 x 8.4, 25.7 x 9.3 cm., with thick brown tomentum, 6 XI 1961, *Cuatrecasas & Paredes* 26536 (US). Vicinity of Guápiles, 300–500 m., seedling, III 1924, *Standley* 37377 (US).

HEREDIA: La Concepción, Llanuras de Santa Clara, 250 m. alt., “cacao de mico,” II 1896, *Donn. Smith* 6457 (BM, US). Santa Clara; 6–7 m. high tree, “cacao de mono,” IX 1896, *Cooper* 10244 (syntype, US) (Photo F. M. 40724).

PUNTARENAS: Terraba, 260 m. alt., forests; caulinar flowers, large cylindrical fruits (30–35 by 10 cm.), “cacao de mico,” II 1891, *Pittier & Tonduz* 3925 (syntype, BR). Boruca, forests 466 m. alt., III 1892, *Tonduz* 6852 (syntype, US).

TRINIDAD (cult.): Imperial College of Tropical Agriculture, *Cuatrecasas & Cope* 25792 (US), 25794 (US).

SURINAM (cult.): Paramaribo, culture garden; tree 10 m., 15 cm. diam., almost horizontal branches, flowers bursting in dense clusters from the trunk and old branches, calyx rusty brown, ligula and staminodes shining lacquer red, 8 IV 1954, *Lindeman* 5725 (U). Ibidem; seeds round, cotyledons white, germination hypogaeic, VIII 1956, *van Suchtelen*, s.n. (US).

BRASIL (cult.): Pará, cultivated and said to be introduced from Venezuela; small tree with purplish flowers, II V 1957, *Pires* 6575 (IAN).

15. *Theobroma grandiflorum* (Willd. ex Spreng.) Schum.

FIGURES 3, 5, 6, 7, 33, 36, 39, 40; MAP 10; PLATE 8

Theobroma grandiflorum (Willd. ex Spreng.) Schum. in Mart. Fl. Bras. 12(3):76, pl. 8, 1886; Jumelle (1899) 28, figs. 14, 15; DeWildeman (1902) 95; Ducke (1925) 131; Ducke (1940) 272, pl. 4, fig. 2; Chevalier (1946) 281; Addison & Tavares (1951) 25, pl. 1, fig. 1, pl. 2, fig. A, pl. 14, fig. 10; Ducke (1953) 11; Baker, Cope & al. (1954) 13, fig. 14; Cuatrecasas (1956) 656; León (1960) 320, 319, fig.

Bubroma grandiflorum Willd. ex Spreng. Syst. Veg. 3:332. 1826.

Guazuma grandiflora (Spreng.) Don, Hist. Dichl. 1:523. 1831.

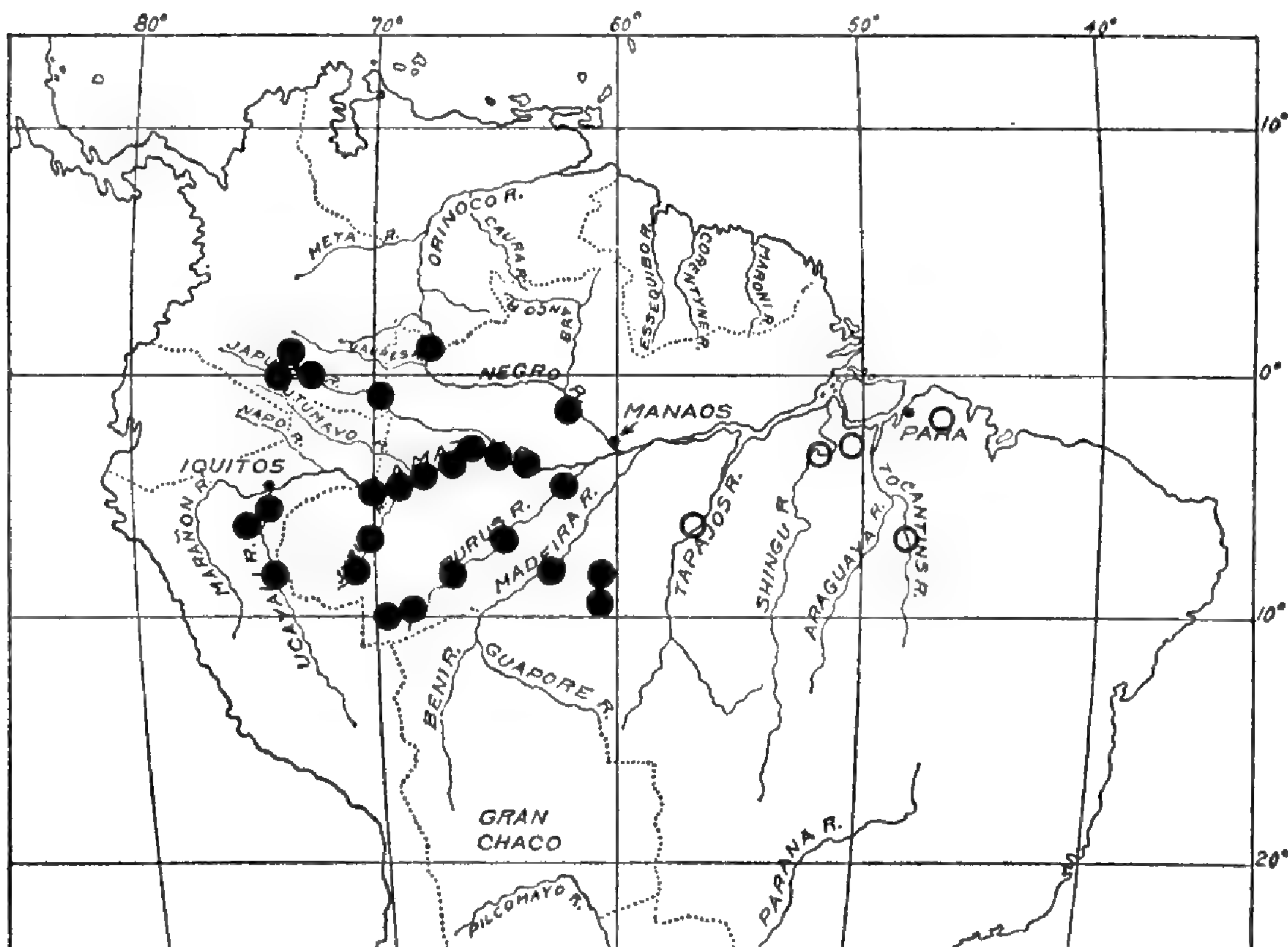
Theobroma speciosum Willd.?, sensu Mart. in Buchn. Repert. Pharm. 35:24. 1830; Linnaea Litt. Bericht 32. 1831, non Willd.

Theobroma macrantha Bernoulli, Uebers. Art. Theobroma 11. 1869.

Theobroma silvestre Spruce ex Schum. in Mart. Fl. Bras. 12(3):76. 1886, as synonym.

TYPE.—*Siber* 4, "Hoffmannseg" in Herbarium Willdenow No. 14352 (B). *Spruce* 1822 (syntype of *T. macrantha* Bernoulli and neotype of *B. grandiflorum* Willd.).

Medium-sized tree, usually 6–10 m. high, reaching up to 18 m.; growth pseudoapical; trunk up to 25–30 cm. in diameter, the bark grayish, granulose, more or less wrinkled, internally rosy or reddish, the wood pale; branches robust, spreading, the superior ascending, the primary ternate; branchlets terete, the terminal rather thick, densely and abundantly lanate-tomentose, the indument ferruginous, floccose,



MAP 10.—Geographical distribution of *Theobroma obovatum* ● and *T. grandiflorum* ○.

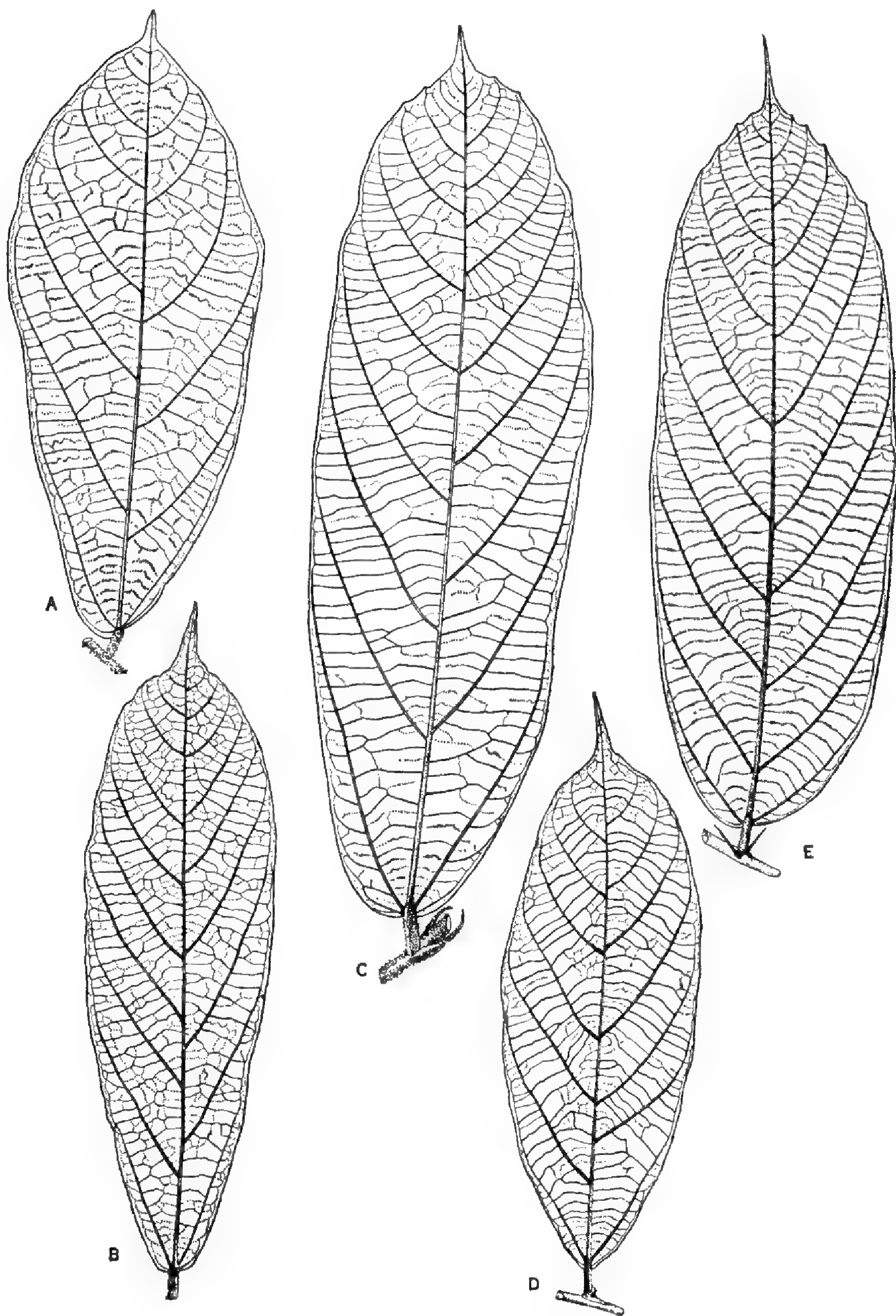


FIGURE 39.—Leaves of *Theobroma*, $\times \frac{1}{3}$: A, *obovatum* (Poeppig s.n.); B, *grandiflorum* (Cuatr. 25780T); C, *grandiflorum* (Killip & Smith 30011); D, *hylaenum* (Araque & Barkley 18C745); E, *subincanum* (Baker 38).

more or less deciduous, the hairs stellate or fasciculate with long, intricate rays, caducous, the surface fulvous, with exfoliating rhytidome, becoming gray, glabrous, and reticulate-rimose; stipules subcoriaceous, rigid, oblong or lanceolate-oblong, obtuse or subacute, nervate-striate, abundantly lanate-tomentose, the tomentum more or less deciduous, 10–20 mm. long, 3–6 mm. broad, persistent.

Leaves firmly coriaceous, medium sized or large; petiole thick, terete, with a dense, thick, ferruginous, lanate tomentum, 7–14 mm. long, 2–5 mm. thick; blades oblong, subobovate-oblong or subelliptic-oblong, more or less attenuate toward the base, this obtuse, rounded, usually emarginate, or subcordate and slightly irregular, abruptly attenuate and acutely acuminate at apex, the margin entire or slightly dentate-sinuate toward the apex, 20–35 (15–60) cm. long, 6–11 (5–16) cm. broad, the acumen 1–2.5 cm. long, glabrous above, green, more or less shining, brownish olivaceous or tabacine when dry, the midrib and secondary nerves filiform, depressed, the tertiary ones slightly marked or obsolete, greenish cinereous, glaucescent, or pale rosy beneath, the costa very prominent, the 9 or 10 pairs of parallel secondary nerves prominent, subascending, near the margin thinner, curved, anastomosing, the lowest pair usually forming a more acute angle and more distally separated from the next, the filiform tertiary nerves prominent, transverse, parallel, the minor nerves and veins forming a fine prominulous reticulum, the costa, secondary, and tertiary nerves glabrous, nitidous, with sparse reddish, callose dots, the reticulum and areoles minutely tomentose, covered by white, minute, intricate, dense, stellate hairs.

Inflorescences small, axillary and extra-axillary on leafy branches, the short cymes reduced to 3–5 flowers or fewer, the branchlets extremely short, ferruginous tomentose, the peduncles robust, 2–5 mm. long, 3-bracteolate at apex, the bracteoles narrowly linear, tomentose, 3–4 mm. long; pedicels robust, rather thick, tomentose, ebracteate, 5–20 mm. long.

Calyx subcymbiform; sepals firm, thick, carnose, ovate-oblong, subacute, about 14–15 mm. long, 6–8 mm. broad, 1.5 mm. thick, united in the lower third, but often the five separated to near the base in two pairs and one free (2S+2S+S), the margin involute, the apex minutely inflexed, thickly stellate-tomentose outside, ochraceous green or ferruginous, rosy or reddish inside, shining, minutely, sparsely, whitish pubescent, at base with minute, thick glandular trichomes, the margin densely and minutely whitish tomentose.

Petal-hoods thick, carnose, whitish or yellowish, often with red lines, obovate, rounded-cucullate at apex, 7-nerved, rugulose without, pubescent, glabrous within, near the base reddish, 6–7 mm. long, 4–6 mm. broad; petal-lamina dark red or crimson, pedicellate, thick,

carnose-coriaceous, trapezoid-elliptical, more or less truncate or slightly retuse, obcordate, minutely puberulous, 4–9 mm. long, 4.5–8.5 mm. wide, abruptly contracted at base into a 4.5–7 mm. long, 1.5 mm. broad pedicel.

Androecium tube 2.5 mm. high, sparsely pilose; staminodes reflexed in bud, spreading in anthesis, crimson, dark red or purplish red, lanceolate, very acute, thick, but somewhat flattened with a marked midrib, 9–15 mm. long, 2–2.5 mm. broad throughout, pilose, especially outside, the abundant hairs rather long, thin, flexuous; filaments 1.7–2 mm. long, thick, pilosulous, very shortly 3-furcate, 3-antheriferous; lobes of the anthers broadly elliptic, 1 mm. long; ovary pentagonous-obovate, densely whitish hirsute-tomentose; styles 2 mm. long, connivent, free to the base.

Fruits falling from tree at maturity, without peduncle, densely covered with a brown tomentum, large, smooth, ellipsoid or obovoid-ellipsoid, rounded at both ends or, rarely, slightly attenuate at apex, umbilicate and conically excavate at base, 16x10–25x12 cm.; pericarp about 1 cm. thick, with: 1) epicarp hard, woody, about 2 mm. thick, covered with a thin, tomentose epidermis, 2) mesoendocarp about 7 mm. thick, softly carnose at maturity with a thin, but firm, inner pellicle limiting the seed cavity; seeds about 50, 5-seriate, each surrounded by a yellowish, acidulous and distinctively scented, fibrous pulp, the inner tegument a delicate pellicle, the testa subcoriaceous, light brown, striped from the remains of the pulp, ovoid, or ellipsoid-ovoid, more or less flattened, 20–30 mm. long, 20–25 mm. broad, 10–12 mm. thick; embryo white marbled, 19–23 mm. long, 16–20 mm. broad, 9–12 mm. thick; cotyledons white; germination hypogeous.

The type of *Bubroma grandiflorum* Willd. ex Sprengel is the specimen No. 14352 of the Willdenow Herbarium in Berlin, received from the Hoffmannsegg Herbarium, collected in Brazil by Siber. This species was transferred to *Guazuma* by G. Don who probably did not see the plant, his description being taken from Sprengel. Schumann found out that *B. grandiflorum* is synonymous with *T. macranthum* described by Bernoulli many years later. The short diagnosis given by Sprengel agrees with *T. macranthum* and the description of the leaves ("amplis oblongis abrupte acuminatis integerrimis") disagrees with any known species of *Guazuma*, which always have serrate leaves. Freitag, who listed *Bubroma grandiflorum* as synonym of *Guazuma ulmifolia* (p. 216), did not see the type. In 1952, Dr. Mildbraed of the Berlin Herbarium wrote me about this type specimen: "Im Herbar Willdenow fehlte unerklärlicherweise der Bogen 14352 mit *Bubroma grandiflorum*." Schumann had seen the type in the Willdenow Herbarium, for which reason I accept his judgment as final regarding the synonymy established by him. Accordingly, I propose *Spruce* 1822 as a neotype

of *B. grandiflorum* Willd. ex Spreng., as it is the first collection cited by Schumann and likewise a syntype of *T. macranthum* Bernoulli.

COMMON NAMES.—Cupassú, with some variations in the spelling or pronunciation throughout its area of cultivation, cupuaçú, cupú-assú, copuassú, cupai-açú. Ducke quoted cupú do matto for wild specimens in the middle Tapajoz River. The Anglo Colombian Cocoa Expedition recorded the following indigenous names (Baker, 1952): Win-cheék-chóo-ai (*Puinave*), Inírida-Guaviare; bawk-pom (*Maku*), Piraparaná, Taraira; maga (*Barasana*), Upper Piraparaná; ñee-aw (*Tanimuka*), Guacaya; cupu-uassú (Brazil-Portug.); ba-dja-na-hoo (*Makuna*), Lower Piraparaná.

USES.—The natives like to eat the acid and agreeably scented pulp which covers the seeds, for which reason cupuassú is very much cultivated or planted in the state of Pará and the eastern section of Amazonas. This pulp is used to prepare soft drinks (vinho do cupuassú) and different kinds of preserves and candy which are exported from Pará and Maranhão. The taste of the pulp is *sui generis*. L. Williams compares it with that of guanábana. Patiño found the odor of it similar to that of the "mate" (*Crescentia cujete*) when beginning its fermentation. The fruits are very much liked by animals, especially by monkeys (macacos), which very often empty the pods to sip the pulp, contributing to the dissemination of the seeds.

DISTRIBUTION.—The known natural area of *T. grandiflorum* is the southern half of state of Pará, Brazil, and adjacent Amazonian Maranhão. It has been found wild only in the rain-forest, on elevated ground in the middle Tapajóz River region (waterfalls of Mangabal and of Itapacurá, *Ducke*), Tocantins River (railroad of Alcobaca, *Ducke*), Guamá River between Ourem and Bragança (*Huber*), Xingú River between Victoria and Altamira (*Ducke*), and Anapú River (*LeCointe*). The tree is always scarce in its natural area.

This medium-sized tree with large leaves, the largest flowers in the genus, and the largest pods among the Brazilian cacaos, is frequently planted or cultivated throughout the states of Pará, Maranhão, and the eastern part of Amazonas to Manaus. It is also occasionally planted outside Brazil in warm lowlands of other tropical American countries, such as Colombia, Venezuela, Ecuador, and Costa Rica. It is found also in tropical botanical and agricultural gardens.

MARTINIQUE: From seeds from Cayenne, *L. C. Richard*, s.n. (P).

BRITISH GUIANA: "Herbarium Benthamianum," *Schomburgk*, s.n. (K).

VENEZUELA: AMAZONAS: Capihuara, Alto Casiquiare, 120 m. alt.; cultivated, small tree up to 8–10 m., subrounded crown, trunk 25 cm. diam., gray bark, inner rose or reddish, wood pale, pulp of fruit used to prepare beverages with similar taste to the guanábana, "cupuasú," 28 V 1942, *Ll. Williams* 15615 (F, US, VEN).

COLOMBIA: VAUPÉS: Monfort; tree 6 m., sepals fleshy, petals maroon, 23 IX 1943, *P. Allen* 3105 (COL, MO, US). Río Vaupés, opposite confluence with Río Papurí, Yavaraté, Salesian Mission São Miguel; tree about 3 years old, growing in full sunlight, beginning to flower, no fruit, 20 II 1952, *Bartley & Holliday* T-46 (COL, US). Río Piraparaná, near confluence with Río Apaporis, river level; young tree 3-4 m., cultivated in Indian garden, 24 VIII 1952, *Baker & Cope* 5 (TRIN).

AMAZONAS: Río Caquetá, La Pedrera, river level; cultivated tree, rather exposed, in the garden of the Orfanatorio, 19 IX 1952, *R. E. D. Baker* 16 (COL, F, TRIN, US). La Pedrera, cultivated, highland; bushy tree 12 ft. tall, petals purple red, calyx light golden brown, staminodes yellowish, 7 X 1952, *Schultes & Cabrera* 17781 (US). Río Ricapuya, tributary of Río Apaporis, river level; 2-3 years, young cultivated tree in Indian garden, 25 VIII 1952, *Baker & Cope* 6 (COL, F, TRIN, US). Leticia, 22 VIII 1946, *Black & Schultes* 46-61 (AMES, F, IAN, NY, U, VEN); tree 8 m., "cupu-assú," cult., 24 IX 1946, *Black & Schultes* 46-III (IAN). Trapecio Amazónico, Amazon River, Leticia, 100 m. alt.; cultivated, "cupuassú," IX 1946, *Schultes* 8178 (AMES, F, US).

BRAZIL: "Catal. Geogr. Pl. Bras. Trop.," *Burchell* 9467 (GH, K, P). Ibidem, *Burchell* 9375 (syntype of *Theobroma macrantha* Bernoulli, K). "Amazon region," *H. A. Wickham*, s.n. (K). "Brazil Cameta," Herb. *Hanbury* 9471 (K).

AMAZONAS: Rio Negro, São Gabriel; arvore 8 m., planta antiga dos sitios, "cupu-assu," 27 XII 1945, *Fróes* 21556 (IAN, K, NY, USDA). Upper Rio Negro basin, Mouth of Rio Xie, cultivated; small tree, staminodes and ligules deep red, rest of flower pink, "cupu-uassu," 29 XI-7 XII 1947, *Schultes & López* 9204 (AMES, F, IAN, US). Rio Negro, prope Barra; "shrub 12-15 ft., flowers only on ramuli, solitary normally ascendant, calyx pinkish within, petals crimson, cucullate, bases yellow white, coronal scales red"; the Munich specimen bears the number 83 on a mounting tape (F. M. Photo 40705), Oct. 1851, *Spruce* 1822 (neotype of *B. grandiflorum*, M; isosyntypes of *T. macrantha* Bernoulli, BM, E, G, GH, K, LE, LD, NY, OXF, P, WU). Manaus, Horto Experimental, 20 m., "cupai-açú," 19 XII 1923, *Luetzelburg* 22007 (M, NY, WU). Manaus, Agricultural Experiment Station, 25 m. alt., cultivated; tree 35-40 ft., inflorescences on main trunk, sepals green without, pink within, petals red, 13 X 1929, *Killip & Smith* 30011 (NY, US). Manaus, Estrada do Aleixo, firm land; tree 6 m., flower red, edible fruit, "cupuaçú," 16 IX 1955, *Francisco* (INPA) 1966 (IAN). Manaus, Hacienda Brasil, 15 m. alt., "cupu-açú," *Luetzelburg* 23287 (M). Manaus, VIII 1906, "cupu-assú," *Labroy*, (P). Three days upstream from Manaus, 300 ft. alt.; grown in semishade; flowers cream colored or dark crimson, growing out of the bark, faintly scented, *Sandeman* 2333 (K). Paraná de Matitins, Rio Putumayo, Iça, between Tarapacá and its mouth (Santo Antonio do Iça, 100 m. alt.); small treelet; calyx very fleshy, green yellow; staminodes white, laciniae flesh red turning brown on fertilization, "cupuassú," 11-18 IX 1946, *Schultes & Black* 8146 (F, IAN). Municipality of Mahacapuru, Solinos River region, terra firma, Lago do Italiano; tree 25 ft. high, 4 inches diam., "cupu-assú," *Krukoff* 1274 (A, BM, G, K, MICH, MO, NY, P, S). Tefé; tree 7 m., flower brownish rose, cult. "cupuaçú," *Black* 47-1502 (IAN).

MARANHÃO: Turyassu, Igapo-wald; Baum 6-15m., Krone gelblich, filaments rot-violett, 31 X 1923, *Snethlage* 300 (F, GH, US).

ACRE (Territorio Federal): Brasilea, in a house in front of the Bolivian town Cobijia, 150 m. alt., "copuassú," cultivated, 5 IX 1954, *Patiño* 163 (GH).

PARÁ: Belém, northeast woods of the Instituto Agronómico do Norte; infected with witches broom, "cupu-assu," 30 X 1942, *Archer* 7734 (IAN, NY, US). Belém, Botanic Garden of the Museu Goeldi; native of the lower Amazon

country; the tree becomes much larger than the cacao and the top is relatively narrower; the fruit resembles the pod of cacao but is much larger and the pulp surrounding the seeds is most delicious; Dr. Huber speaks of it as the most important native fruit of Pará; "cupuaçú," 25 VI 1908, *C. F. Baker* 62 (A, C, E, GH, LE, MICH, MO, P, U, US, NY). Museu Goeldi, 23 XI 1945, *Pires & Black* 744 (IAN). Jardim Botânico do Museu Goeldi; large tree, calyx with red marks inside base, spatulate portion petal dark red, fruit edible, "cupuaçú," 11 VIII 1942, *Archer* 7549 (F, IAN, K, US). Ibidem; small tree, leaves gray both surfaces, flowers large, cauliflorous, calyx white yellow, staminodes deep red, petals pinkish, very showy, a profusion of flowers, cultivated, 15 VII 1946, *Schultes* 8065 (AMES, US). Horto Botânico do Pará, XI 1903, "cupuassú," *Huber* 4008 (BM, G). Ibidem, "cupuassú," XI 1903, *Siqueiros* 4008 (MG). Belém, "in urbe cultum; arbor parva floribus brunnescentibus centro albido," "cupuassú," 16 X 1940, *Ducke* 598 (F, IAN, MG, MO, NY, US). Ibidem, III V 1929, *Dahlgren & Sella* 438, 634 (F), "cupu-assu," *Dahlgren & Sella* 733, 739 (F, GH, US). Vicinity of Pará, 1 VII 1908, *C. F. Baker* 421 (BM, C, F, L, U, WU). In sylva prope Barba et alibi, VIII 1828, *Riedel* 1373 (A, LE, S, US). "Brasilia, Borbar," *Riedel*, s.n. (OXF). Bôa Vista, on the Tapajós River, Aramanahy River, "cupuassú," *Monteiro de Costa* 121 (F). Taperinha bei Santarem, kultiviert; aus dem Fructen wird Marmelade bereitet, kleiner Baum, "Cupu-assú," 18 IV 1927, *Ginzberger & Zerner* 800 (F, WU). "Habitat in sylvis udis umbrosis ad Para, Dr. Martius Iter Brasil. Jul. 323," *Martius* [874] (M). "Prov. Paraensis ad Para, Dr. Martius Iter Brasil. 323," *Martius* [875], [876] (M) (Photo F. M. 40706). Ibidem, *Martius* [873] (M) mixed with *T. guianense* in Photo F. M. 19641). Pará, "Bresil-Martius," *Martius* (G, P). Tapana, near Pará, woods; 30-40 ft. tall, appendages purplish red, clearing, fruit edible, 29 X 1929, *Killip & Smith* 30320 (NY, US). Forêt des collines du Mangabal, moyen Tapajós, Cachoeira do Mangabal, "cupú do matto," 5 IX 1916, *Ducke* 16458 (BM, G, MG, P).

RIO DE JANEIRO: Rio Janeiro, cultivated, "cupú assú," *Glaziou* 9643 (C, P).

PERU: LORETO: Caballo Cocha, on the Amazon River, "cupuassú," VIII 1929, *Ll. Williams* 2401 (F).

TRINIDAD: St. Augustine, Imperial College of Tropical Agriculture, River State Diego Martinez, Field 2; trunk 20 cm. diam. at base, leaves coriaceous dark green above, green beneath, fruits ellipsoid, densely tomentose, brown ferruginous, 11 x 17, 11.5 x 18.5, 11.5 x 16.5, 12 x 19, 12 x 19.5, 12.5 x 19 cm., with 47-50 seeds, pulp yellowish with special scent, cultivated, brought from Belém do Pará, 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25780 T (US). Ibidem; tree with larger and slightly attenuate fruits at apex, 10.7 x 22, 11.1 x 21.5, 11.8 x 25 cm., 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25781 T (US). Saman Plot, cultivated from seeds brought from Pará; trunk 30 cm. diam., the diameter reducing progressively upwards from one cluster of branches to the next, primary branching ternate, from the base, apical growth, bark greenish brown, granulate-lenticellate, minutely rimose, sepals 1.5-2 mm. thick, greenish ochraceous outside, whitish and pink at base inside, hoods white yellowish or dirty whitish, the margin and the base inside purplish, lamina carnose, dark red, later red brown, staminodes star-patulous, red purplish becoming red brownish, styles united whitish, ovary white, hirsute-tomentose, 2 IX 1961, *Cuatrecasas & Cope* 25801 (US).

16. *Theobroma obovatum* Klotzsch ex Bernoulli

FIGURES 33, 35, 39, 40; MAP 10

Theobroma obovatum Klotzsch ex Bernoulli, Uebers. Art. *Theobroma* 14, pl. 7, fig. 3. 1869; Ducke (1935) 132; (1940) 271, pl. 5, fig. 1; Chevalier (1946) 280; Addison & Tavares (1951) 25, pl. 1, fig. 2, pl. 2, fig. B, pl. 3, fig. 2, pl. 4, fig. B, pl. 11, fig. 1; Ducke (1953) 10; Cuatrecasas (1956) 657; Baker, Cope & al. (1954) 12, fig. 15; León (1960) 322, 319, fig.

Theobroma sylvestre sensu Huber, Bull. Herb. Boiss. II, 6: 273. 1906, non Mart.

TYPE.—Maynas, Peru, *Poeppig*.

Rather small tree up to 15 m. high; growth pseudoapical; trunk 10–25 cm. in diameter; primary branches ternate, the inferior horizontal, the upper ascending; terminal branchlets slender, when young ochraceo-ferruginous, densely lanate-tomentose, the intricate, long, stellate hairs more or less floccose, deciduous, when older glabrate, pale brown or pale gray, the rhitidome somewhat scaly; stipules narrow-linear, subulate, acute, tomentose, 3–5 mm. long, 0.5–1 mm. wide, soon deciduous.

Leaves chartaceous, flexible, variable in size; petiole mediocre, subterete, transversely rimose, densely and thickly lanate-tomentose, ferruginous, when old the indument appressed, grayish, 4–15 mm. long; blades obovate-elliptic or obovate-oblong, more or less narrowed to the very asymmetrical and rounded base, more abruptly attenuate and cuspidate at apex, entire or slightly sinuate at margin, 7 x 3 to 38 x 13 cm., including the 0.5–3 cm. long acumen, varying very much in size on the same branch, when very young stellate-pilose above, then glabrous, pale olivaceous or pale brownish, shining, the main nerves depressed, filiform, the others obsolete, pale ochraceous or pale cinereous beneath, glaucescent, the costa very prominent, the 5–7 secondary nerves on each side prominent, curved-ascending, near the margin arched anastomosing, the lower pair usually forming an acute angle, ascending and more distally separated from the others, the transverse tertiary nerves thin but prominent, the minor veins forming a prominent conspicuous reticulum, the costa and the principal lateral nerves covered when young, mainly towards the base, by a floccose deciduous indument of ochraceous, entangled, stellate hairs, in time becoming glabrous, shining, marked with minute callose, reddish, sparse dots, the tertiary nerves also glabrous, the minor veins, reticulum, and areoles covered by minute, white, stellate hairs forming an appressed, whitish tomentum.

Inflorescences very small, axillary or in exfoliated, thin branchlets, the axis and branchlets of the cymes very reduced, ochraceous-ferruginous, lanuginose-tomentose; peduncles 2–7 mm. long, 3-bracteolate at apex; pedicels 3–8 mm. long, somewhat thicker; bracteoles

linear, 1.5–2 mm. long; buds globose, also ochraceous-lanuginose and woolly-tomentose.

Sepals thick, ovate, subacute, slightly involute-marginate, about 6–7 mm. long, 3–4 mm. broad, united 1 mm. at base, rosy or reddish inside, subglabrous, glandular at base, 3–5 nerved, the margin minutely whitish tomentose, rather woolly outside, stellate-tomentose, spreading in anthesis; petal-hoods yellowish or reddish obovate, rounded cucullate and slightly retuse at apex, with 7 prominent nerves and copious, spreading, minute hairs inside, subglabrous with few, slender, flexuous hairs outside, 3–3.5 mm. long, 2.5 mm. broad; petal-lamina deep red, rather thick, suborbicular, often retuse at apex, abruptly contracted into a pedicel at base, pilose at margin, and with very sparse, flexuous, slender hairs on the inner side, 3.5 mm. long, 4 mm. broad; pedicel red, 0.6 mm. wide with sparse, slender hairs, 2.5 mm. long.

Androecium tube about 1.5 m. high, glabrous; staminodes laminar, thick-membranaceous, deep red, oblong-elliptic, rounded and often emarginate at apex, attenuate near the base, with a conspicuous medial nerve and thin, flexuous, subspreading hairs distributed throughout, especially on the margins, 5–6 mm. long, 2.5–3 mm. broad; filaments thick, glabrous, 1.5 mm. long, shortly 3-furcate, 3-antheriferous; anther lobes ellipsoid, 0.4–0.5 mm. long; ovary ovoid, 1.5 mm. long, densely tomentose-hirsute; styles glabrous, 5 mm. long, united only at base.

Fruit obovoid-ellipsoid, rounded at apex, contracted at base, greenish, when ripe brown yellowish, 5–7 cm. long, 3–4 cm. broad, the pericarp thin-coriaceous densely covered with acute, hard warts and sparse stellate hairs, when dry about 1.5 mm. thick; seeds 16 mm. long, 9 mm. broad; germination hypogeous.

COMMON NAMES.—Cabeça de urubú is the most common and widespread. Also, the following have been locally recorded: copu-ai, cupu-curúa, cupurana, cacao de macao, urubú-acain, cabeça de Umbú.

Win-cheék (*Puinave*), Inírida-Guaviare; ma-oo-hee-rée (*Kabuyarí*) (Rio Cananarí) (Angl. Col. Cocoa Exped., Baker 1952).

DISTRIBUTION.—Spread throughout the western part of the Amazon basin, on elevated ground and humid, fertile soil of rain forests. In Brazil it is frequent in the western half of Amazonia, the easternmost localities known being Teffé, on Rio Solimoes and Rio Jau, a tributary of the Rio Negro (*Ducke*). The Anglo-Colombian Cacao Expedition found it (although not abundantly) in the rivers Caguán, upper and lower Caquetá, and the Putumayo (Report, 1954, 12, 13). In Peru goes as far as the lower parts of Río Huallaga and Río Ucayali, Río Itaya, and also Putumayo.

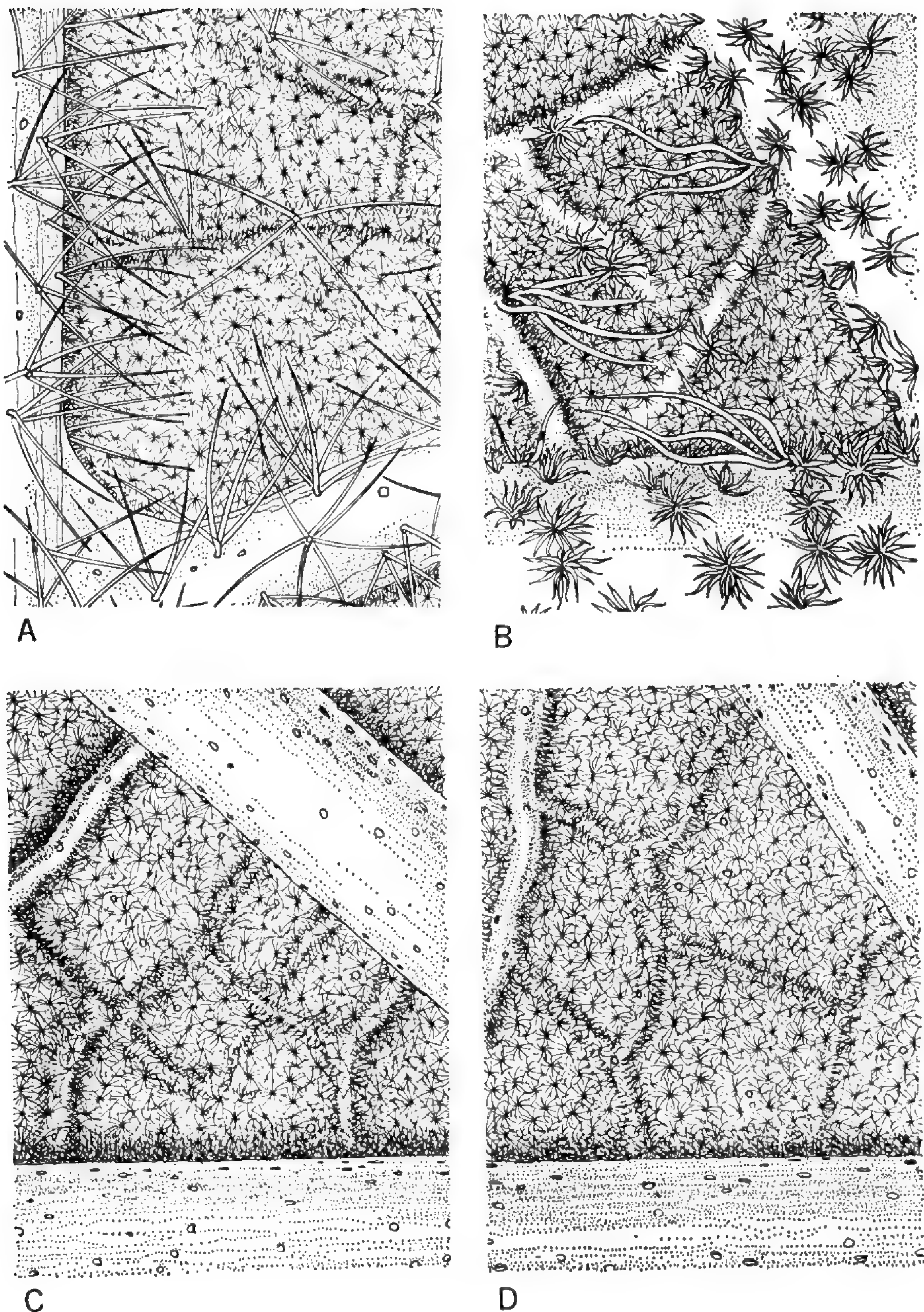


FIGURE 40.—Detail of indument on the underside of leaf in: A, *Theobroma simiarum* (Standley 37377) from seedlings; B, *T. simiarum* (Pittier 7731), from adult branches; C, *T. grandiflorum* (Killip & Smith 30011); D, *T. obovatum* (Ducke 265). A $\times 20$, B $\times 30$, C and D $\times 40$.

Theobroma obovatum is a rather small tree with a crowded, leafy crown, easy to recognize by its small, ellipsoid-obovoid fruits constricted at the neck, with thin, fragile, granulate or verrucose pericarp, usually green but becoming brownish yellow when ripe. Also characteristic are its light, papery, asymmetrical, oblong-obovate leaves with a close, white or cinereous monotrichous tomentum beneath; when very young the upper side, the principal nerves as well as the petioles, stipules, and twigs, are covered with an ochraceous brown or orange, easily removed down, composed of long, deciduous, stellate hairs. The fruit when ripe separates from the pedicel and falls.

Schumann did not know the species, for it is lacking in his herbarium; he included the name *T. obovatum* as a synonym of *T. subincanum* in his treatment in the Flora Brasiliensis (p. 77).

Huber knew the species well, although he called it *T. sylvestre*, confusing and misinterpreting Aublets figure of *Cacao sylvestris*. Ducke also knew *T. obovatum* and its distribution very well, but he thought that *T. sylvestre* Mart. was a synonym.

COLOMBIA: PUTUMAYO: Río Caucayá, Río Leguízamo, Laguna Primavera; tree 15 m., 3 IV 1953, *Holliday & Cope* T/90 (COL, TRIN, US). Ibidem; tree 10 m., flowering, on elevated land above river, 5 IV 1953, *Holliday & Cope* T/95 (COL, TRIN, U, US).

CAQUETA: Río Caguán, camp 4, 27 IV 1953, *Holliday & Cope* T/119 (COL, TRIN, US). Ibidem; found on sloping land, 30 ft., above river, tree 6 m., jorquettes arising symmetrically, 26 IV 1953, *Holliday & Cope* T/114 (COL, TRIN, US).

AMAZONAS: Río Caquetá, La Pedrera, river level; tree 10 m., native in forest on the riverbank, 7 X 1952, *Baker & Cope* 30 (COL, F, TRIN, US). Ibidem; tree 7-8 m. in forest river-bank, presumed native, jorquettes regularly of three branches growth continuing from above, young twigs and leaves with caducous fuzz, flowers pale crimson, 5 X 1952, *Baker & Cope* 27 (COL, F, TRIN, US). Ibidem; large tree 30 ft. high; calyx lobes light outside and pinkish inside, petals dark purplish red, diameter 9-10 inches, 5 X 1952, *Schultes & Cabrera* 17775 (US). Río Caquetá, Remolino; tree 6-8 m., no flowers but had two ripe pods, 2 V 1953, *Holliday & Cope* T/123 (COL, TRIN, US). Trapecio Amazónico, Loretoyacu River, 100 m. alt., XI 1945, *Schultes* 6921 (F).

BRAZIL: PARÁ: Belém, Jardim Botânico do Museu Goeldi; small tree, "cacau cabeça de urubú," cultivated, 11 VIII 1942, *Archer* 7537 (USDA, IAN). Ibidem; arvore no. 482, 22 XII 1958, *Cavalcante* 339 (MG, US). Ibidem, *Pires & Black*, s.n. (BH), 743 (IAN). Ibidem (Río Purús, loco dicto Bom Logar oriuntur, J. Huber anno 1904 accedit); arbor parva floribus atrorubris, fructus maturitate flavidis, "cabeça de urubu," 4 II 1926, *Ducke* 21044 (G, K, P, U, US). Ibidem, *Ducke* 265 (A, F, K, MO, S, US). Belém, cultivado in Instituto Agronómico do Norte, "cabeça de urubú," *Pires, Nilo, & Silva* 4339 (IAN, UC, US).

AMAZONAS: San Antonio do Iça, matta, 27 IX 1906, *Ducke* 7704 (MG). On the Rio Negro, *Schomburgk* 870 p.p. (L). Municipality São Paulo de Olivença, near Palmares; tree 35 ft. high, trunk 4 inches diam., terra firma highland, 11 IX-26 X 1936, *Krukoff* 8275 (A, BM, FE, F, G, K, MICH, MO, P, S, U, US, USDA, Y). Basin Rio Madeira, Municipality Humayta, near Tres Casas, on

varzea land, shrub 25 ft. high, "cabeça de umbú," 14 IX–11 X 1934, *Krukoff* 6263 (A, BM, F, GOET, K, LE, MICH, MO, S, U, US, Y). "Amazonas Ega," *Poeppig* 2746 p.p. (LE). "Brasilia in sylvis circum Ega, 1831," *Poeppig*, s.n. (WU). Amazonas; Bocca et Teffé, matta, "cabeça de urubú," 27 X 1904, *Ducke* 6823 (BM, G, MG, P, US). Teffé, matta virgen; tree, flower white, "copu-ai," 22 IX 1947, *Black* 47–1496 (IAN). Igarapé Jandiatuba, lowland, border of the river, 14 I 1949, *Fróes* 23926 (US, IAN). Arredodes de Fonte Boa, terra firma alta; arvore media, "cupurana," "cupu-curua," 12 IV 1945, *Fróes*, 20646 (F, K, IAN, USDA). Rio Juruá, Juruá Miry; Baum 3–9 m., Blumen dunkelpurpurn, VIII 1901, *Ule* 5637 (G, HBG, K, MG, L). Purús, Monte Verde, "cacao de macaco," II 1904, *Goeldi* 4226 (MG). Rio Acre: Antimari, matta, 31 III 1904, *Huber* 4295 (BM, G, MG, P, US). Upper Amazon, Paranary; low tree, petals purple, stamens yellowish, staminodia yellow, "urubú-acaim," 20 X 1924, *Traill* 61 (K, P).

ACRE: Basin Rio Purús, near mouth of Rio Macauhán (tributary of Rio Yaco), Lat. 9°20' S, Long. 69° W, on terra firma; tree 35 ft. high, 9 VIII 1933, *Krukoff* 5388 (A, G, K, MICH, MO, S, U, US). Ibidem; shrub 40 feet high, 3 IX 1933, *Krukoff* 5759 (A, BM, F, G, K, MICH, MO, S, U, US).

MATO GROSSO: Machado River region, source of the Jatuarana River; tree 45 ft. high in terra firma, "cupuarana," XII 1931, *Krukoff* 1668 (A, BM, G, K, F, MICH, MO, S, U, UC).

GUAPORE: Porto Velho, km. 8, matta on elevated ground; small tree, 17 VI 1952, *Silva* 155 (IAN).

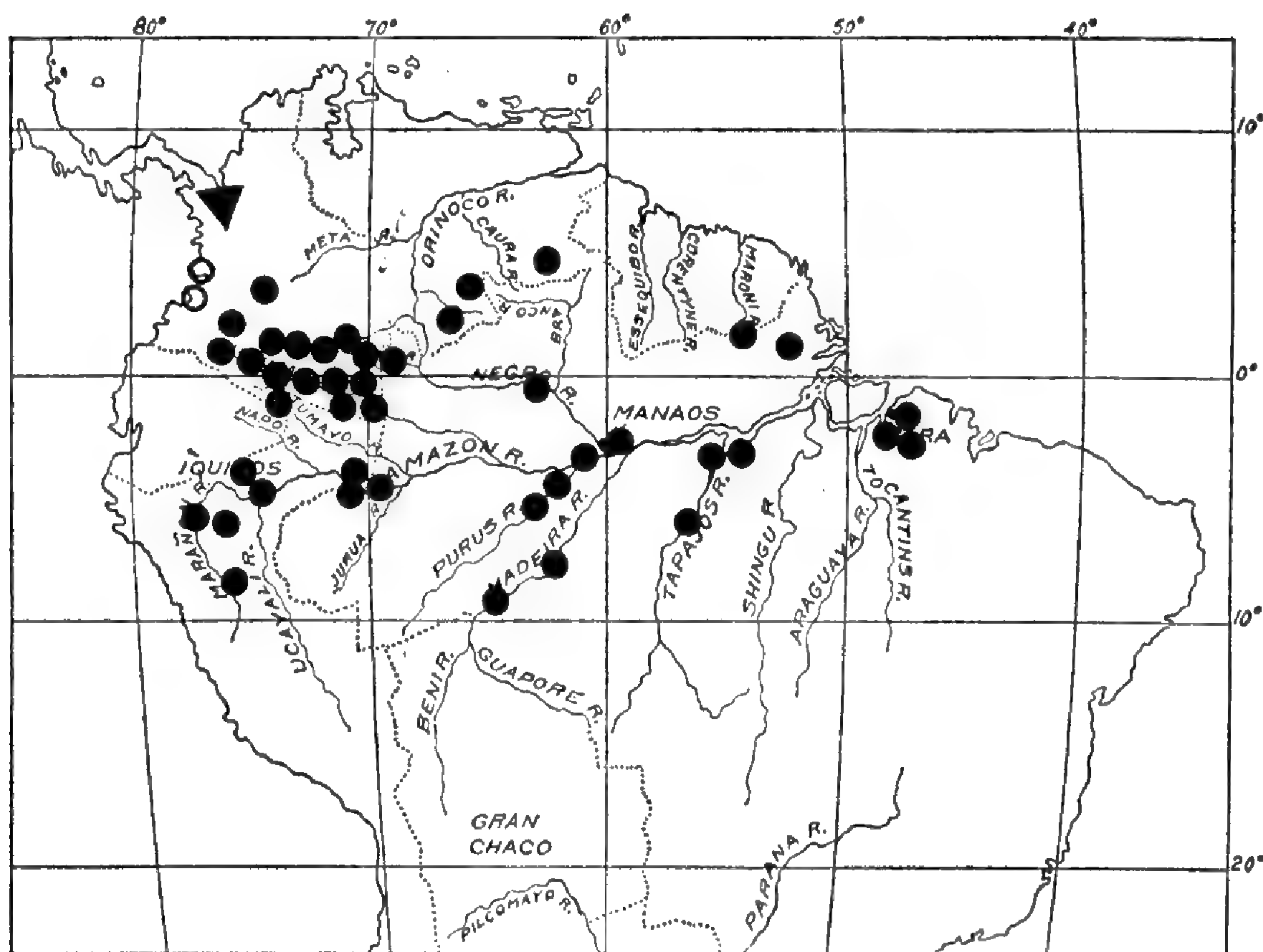
PERU: LORETO: Along Río Itaya, Río Masana, 8 V 1929, *Ll. Williams* 161 (F). Forest of Río Itaya, 3 V 1929, *Ll. Williams* 230 (F, US). Lower Río Huallaga, Puerto Arturo, Yurimaguas, 155–210 m., medium-sized tree, forest, 20 XI 1929, *Ll. Williams* 5268 (F, US). Balsa-puerto, 220 m., forest; tree 4 m., flowers wine red, IV 1933 *Klug* 2983 (A, BM, G, GH, K, F, MO, S, US). Maynas, in sylvis circum Yurimaguas, 1831, *Poeppig* 1845 (G). Maynas 1831, *Poeppig* 2352 p.p. (lectotype, WU; isosyntypes, F, GOET, G, LE, P). Stromgebiet des Ucayali, von 10° S bis zur Mündung, 1923, *Tessmann* 3433 (G, S). Rain forest of the Amazon basin, 230 m., 40 km. south of Pucallpa, 24 VII 1957, *Ellenberg* 2551 (L). Bank of Río Putumayo, opposite Puerto Leguizamo; sucker of large flowering tree, leaves rather large, 7 IV 53, *Holliday & Cope* T/98 (COL, TRIN, US).

TRINIDAD (cult.): Imperial College of Tropical Agriculture, River State Diego Martínez, Field 19; primary branching ternate; growing pseudoapical; branchlets and twigs ochraceous lanate-tomentose, leaves thin, flexible, very pale, with costa and secondary nerves yellow green, with woolly, floccose, deciduous tomentum beneath, green above, 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25783T (US). Ibidem; trunk 15 cm., bark lenticellate-granulate; branching ternate; terminal branchlets light brown or brownish ochraceous, lanate-tomentose, crown very branched and leafy, the lower branches horizontal, the upper ones ascending, young, tender, terminal leaves hanging, light yellowish green, 1 IX 1961, *Cuatrecasas & Cope* 25788 (US).

17. *Theobroma subincanum* Mart.

FIGURES 29, 33, 35, 39, 41; MAP 11; PLATES 9, 10, 11

Theobroma subincanum Mart. in Buchner, Repert. Pharm. 35:23. 1830; Linnaea Litt. Bericht, 32. 1831; Bernoulli (1869) 13; Schumann in Mart. (1886) 77; Jumelle (1899) 27 (in part); Huber (1906a) 274; Ducke (1925) 132; (1940) 272, pl. 4, fig. 1; Addison & Tavares (1951) 25, pl. 3, fig. 1,



MAP 11.—Geographical distribution of *Theobroma subincanum* ● and of its vicariants at the western side of the Andes, *T. hylaeum* ▲ and *T. nemorale* ○.

pl. 4, fig. A, pl. 11, fig. 3; Ducke (1953) 10; Cuatrecasas (1956) 699; Baker, Cope, & al. (1954) 12, fig. 13.

Cacao sylvestris Aubl. Pl. Guian. 2:687, pl. 276. 1775.

Cacao guianensis Aubl. Pl. Guian. 2:684. 1775, pro parte (*tantum folia*).

Theobroma sylvestris (Aubl.) Don, Hist. Dichl. Pl. 1:622. 1831, non Mart. 1830; Chevalier (1946) 279; Lemée (1952) 380; León, (1960) 322, 321, fig.

Theobroma ferruginea Bernoulli, Uebers. Art. Theobroma 13. 1869.

Theobroma alba Ruiz & Pavón, Fl. Peruv. Chil. 6, pl. 68, ined.

TYPES.—Amazonas, Brazil, *Martius*. French Guiana, *Aublet* (of *Cacao sylvestris*). Peru, *Ruiz & Pavón* (of *T. ferruginea*).

Medium-sized tree commonly 6–12 m. tall, at times up to 20 m. high, the trunk 15–20 (–30) cm. in diameter, with gray, almost smooth bark, older bark rugose-rimose, reddish within, the wood whitish, darker toward the center; growth pseudoapical; primary branches ternate, grayish, spreading; juvenile branchlets covered by a dense ferruginous tomentum of stellate hairs, when older glabrescent, pale brownish or brown, somewhat rugose, rimose-reticulate; stipules narrowly linear, densely ferruginous-tomentose, 5–7 mm. long, 1 mm. wide, soon deciduous.

Leaves firmly coriaceous, rather thick and large; petiole robust, subterete, densely and appressed ferruginous-tomentose, 8–15 mm. long; lamina elliptic-oblong or subobovate-elliptic-oblong, very little

attenuate to the base, slightly unequal, rounded or very obtuse, emarginate or rarely cordate at base, somewhat narrowed or rounded and abruptly acuminate at apex, sometimes blunt, entire, or near the apex dentate-sinuate, 16–40 cm. long, 5–20 cm. broad, the acumen acute, 1–3 cm. long, when very young ferruginous-tomentose throughout, but soon glabrescent above, when adult glabrous above, green, somewhat brownish olivaceous when dry, the costa and the lateral nerves depressed, filiform, the lesser veins obsolete, cinereous beneath, the veins more or less tawny or ferruginous, the costa thick, very prominent, the 9 or 10 pairs of secondary nerves very prominent, subascending, thinner near the margin, decurrent, the superior arched, anastomosing, the basal pair often straighter and forming a more acute angle, the transverse tertiary nerves prominent, the minor ones and small veins prominulous, minutely reticulate, the midrib, major nerves, and reticulum more or less densely covered by mediocre, reddish or tawny stellate hairs, the areoles between the veins with a dense whitish indument of very small, delicate, intricate, stellate hairs.

Inflorescence small, few-flowered, axillary or extra-axillary on leafy branches; cymes with 3–9 fasciculate branchlets, usually 1–3-flowered; peduncles 2–8 mm. long, with 3 bracteoles at apex, the bracteoles subulate, about 3 mm. long, deciduous; pedicels 3–6 mm. long, thicker than the peduncle; buds ovoid-globose; sepals thick, carnose, ovate, acute or subacute, densely stellate-tomentose outside, ferruginous, the margin minutely whitish tomentose, shining inside, purplish or red, subglabrous with minute, crowded, oblong-capitate, glandular hairs at base, near the margin slightly pubescent, 8–9 mm. long, 3–4 mm. broad, united at base for 2 mm., subpatulous.

Petal-hoods thick-membranaceous, pale yellow and red striate, obovate, rounded-cucullate at apex, slightly emarginate, 7-nerved, inside minutely hirtulous, glabrous outside except for the puberulous margin, 3–3.5 mm. long, 2–2.4 mm. broad; petal-lamina pedicellate, carnose, thick, rigid, red, suborbicular, 2–2.5 mm. long, 2.2–4 mm. broad, with slightly retuse apex, slightly pilose at margin, the hairs very slender, flexuous; pedicel 2 mm. long, compressed, pilose.

Androecium tube 1.5–1.7 mm. long, glabrous; staminodes laminar, red, lanceolate-oblong, acute or subacute, with marked midrib, subglabrous with sparse flexuous hairs at margin, 6–7.5 mm. long, 2 mm. broad; filaments rather thick, glabrous, about 1.5 mm. long, arched, very shortly 3-furcate, 3-antheriferous, the anther cells ellipsoid, about 0.5 mm. long; ovary ovoid-oblong, 1.3 mm. long, glabrous, with very sparse, minute, granulate dots; styles 1.5 mm. long, connivent.

Fruit ellipsoid, light green, tawny or orange at maturity, smooth, oblong-ellipsoid or obovate-ellipsoid, rounded at apex, often more or less narrowed at base, 7.5–11.5 cm. long, 5–6.6 cm. broad; pericarp

coriaceous, rigid, hard, 3–4 mm. thick, the woody epicarp 1–2 mm. thick, covered by a brown, thin, appressed, stellate-tomentose indument; seeds ellipsoid-oblong or ovate-ellipsoid, 1.8–2.3 cm. long, 12–16 mm. broad, 8–11 mm. thick, the surrounding pulp rather slightly sweet, scentless, white, becoming yellowish; cotyledons white; fruiting peduncle 1–1.5 cm. long, 0.5–1.0 cm. thick; germination hypogeous.

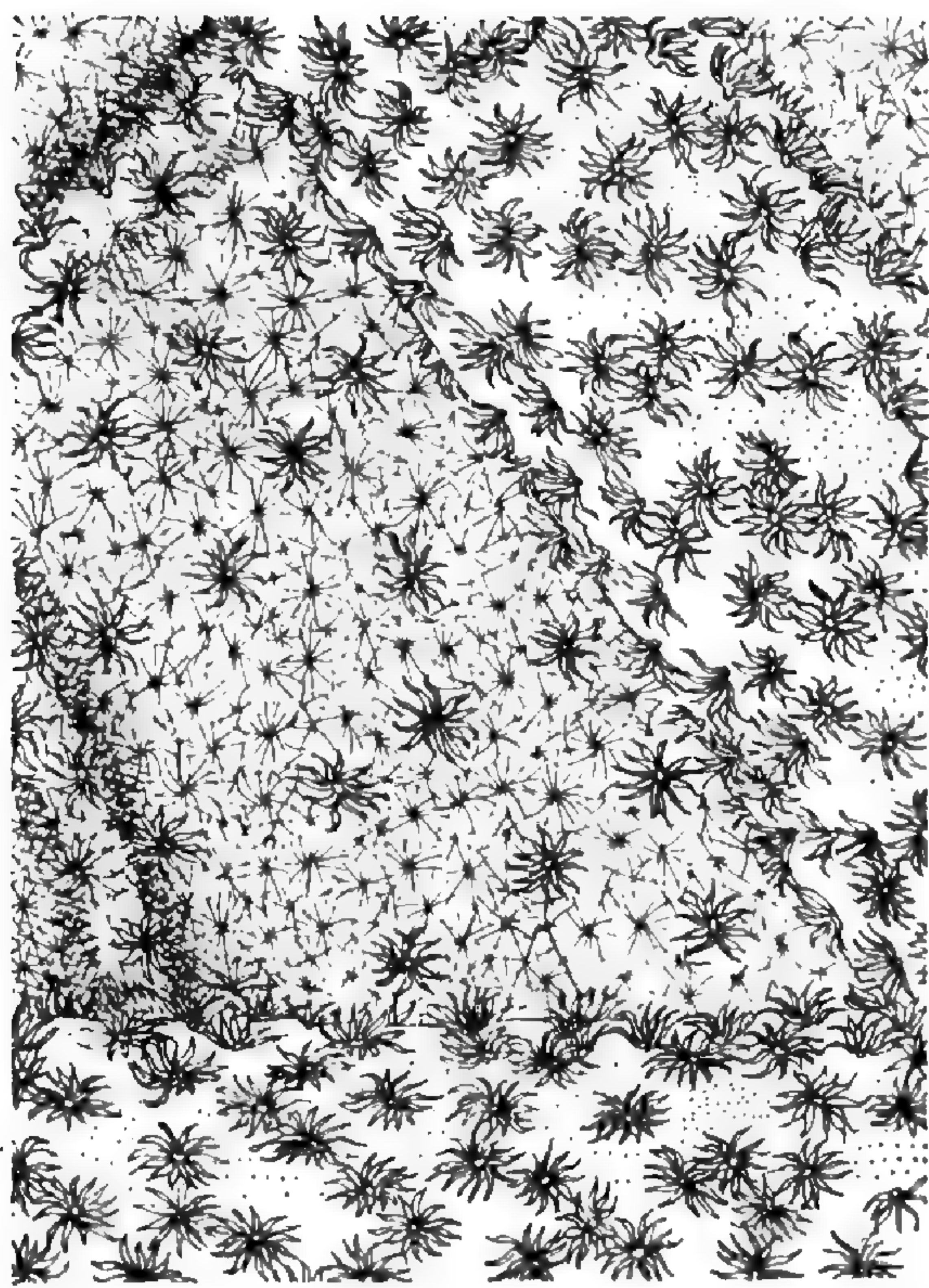
COMMON NAMES.—The commonest names in Brazilian Amazonia are cupuí and cupuaí. Other names or other ways of spelling and pronouncing the former are: copuí, copuaí, cupuhy, cupuahy, cupuy do Igapó, cupuarana, cupú do matta, cupú-assuy, cupú-assú-rana. In Colombia, Venezuela, and Peru this species is usually called cacao de monte or cacao silvestre, and also cacao rana (Orinoco valley), yurac-cacao (Yurimaguas), uchpa-cacao, cacao-ceniza (Peru), cacao blanco (Peru, *Ruíz & Pavón*). Indian names recorded are: abekará (*Makuna*, Vaupés, *García Barriga*), padama (*Arekuna*, Venezuela), cumalá (Peru). The Anglo-Colombian Cocoa Expedition (Baker, 1952) recorded the following indigenous names: Win-cheék (*Puinave*), Inírida-Guaviare; bawk (*Maku*), Piraparaná-Taraira; poo-hoo (*Barasana*), Upper Piraparaná; a-ba-ka-ra (*Makuna*), Lower Piraparaná Popeyaca; mah-we-re (*Yukuna*), Miritiparaná; no-tór-ree-ka (*Tanimuka*), Guacaya; too-soo (*Yauna*), Lower Piraparaná; ma-oo-hee-reé (*Kabuyarí*), Canarari; wa-kó (*Kubeo*), Cuduyarí; wah-pek-la (*Tukano*), Papurí; a-sö-ya-ee (*Piratapuya*), Papurí; wa-be-ga-ra (*Desano*), Papurí; wa-be-ka-ra (*Siriano*), Paca; ma-wé-roo-da (*Kuripaka*), Guainía.

USES.—Although this species gives an acceptable chocolate it is practically never used by the natives. The slightly sweet and scentless pulp is occasionally eaten or sucked; it is very much sought by animals, especially monkeys.

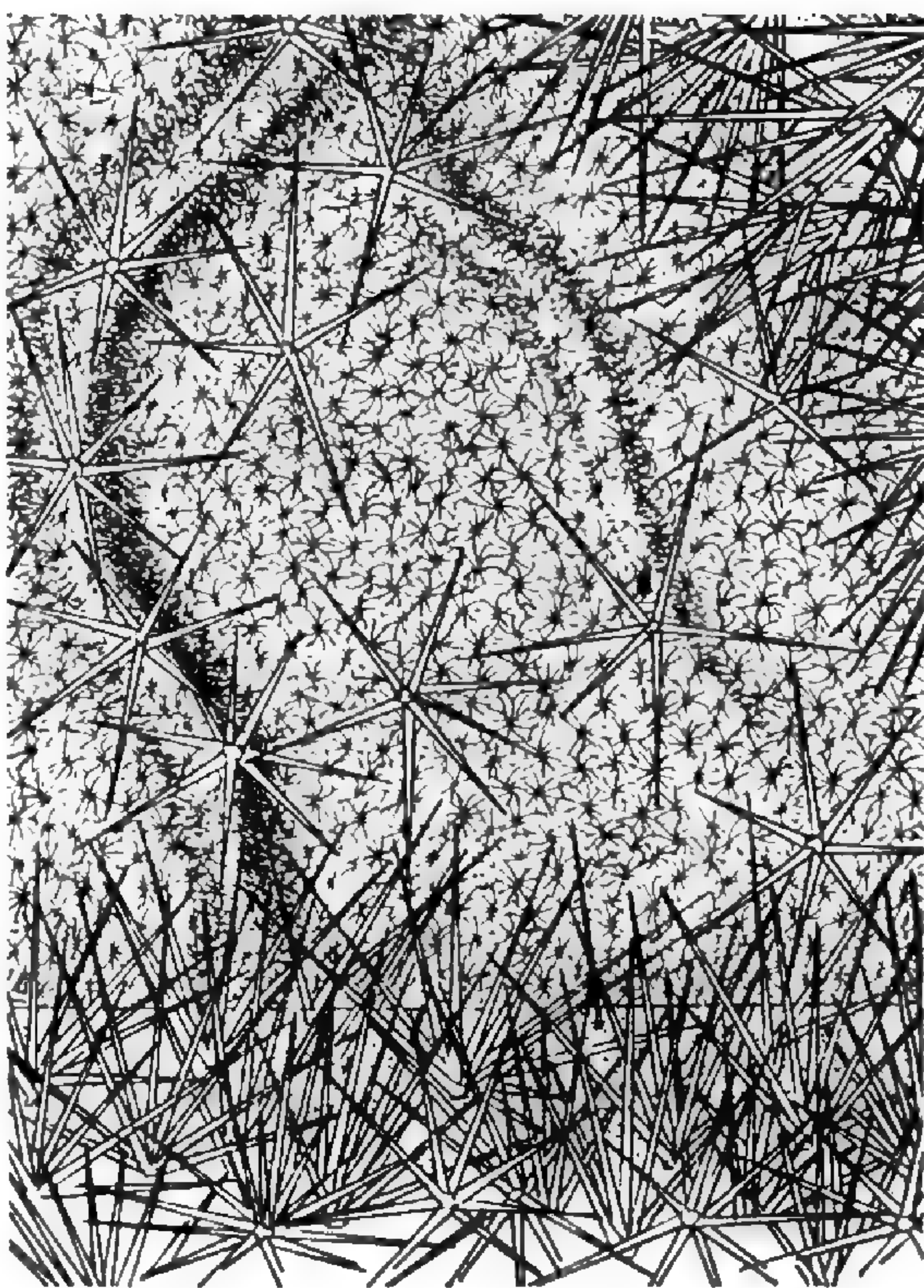
DISTRIBUTION.—Widespread throughout Amazonia from Pará to the most western tributaries of the Amazon River, the upper Orinoco range, and the Venezuelan and French Guayanas; frequent in the shade of the Hylaeian rain forests, in noninundatable lowlands, often on rich and humiferous soil but ascending small hills on sandy grounds, along creeks and small rivers. *Theobroma subincanum* is the species of most frequent and abundant occurrence and with the broadest area of distribution, other than *T. cacao*.

COLOMBIA: META: Acacias, Canaima, farm 350 m. alt., cultivated, 18 XI 1951, *Patiño* 22 (F). Sierra de la Macarena, trail from Río Guéjar to Caño Guapayita, Caño Yerli, 500–600 m. alt.; tree about 35 ft. tall, flowers deep red, fruit ripening brown, leaves rusty beneath, 20–28 XII 1950, *Idrobo & Schultes* 776 (COL, IAN).

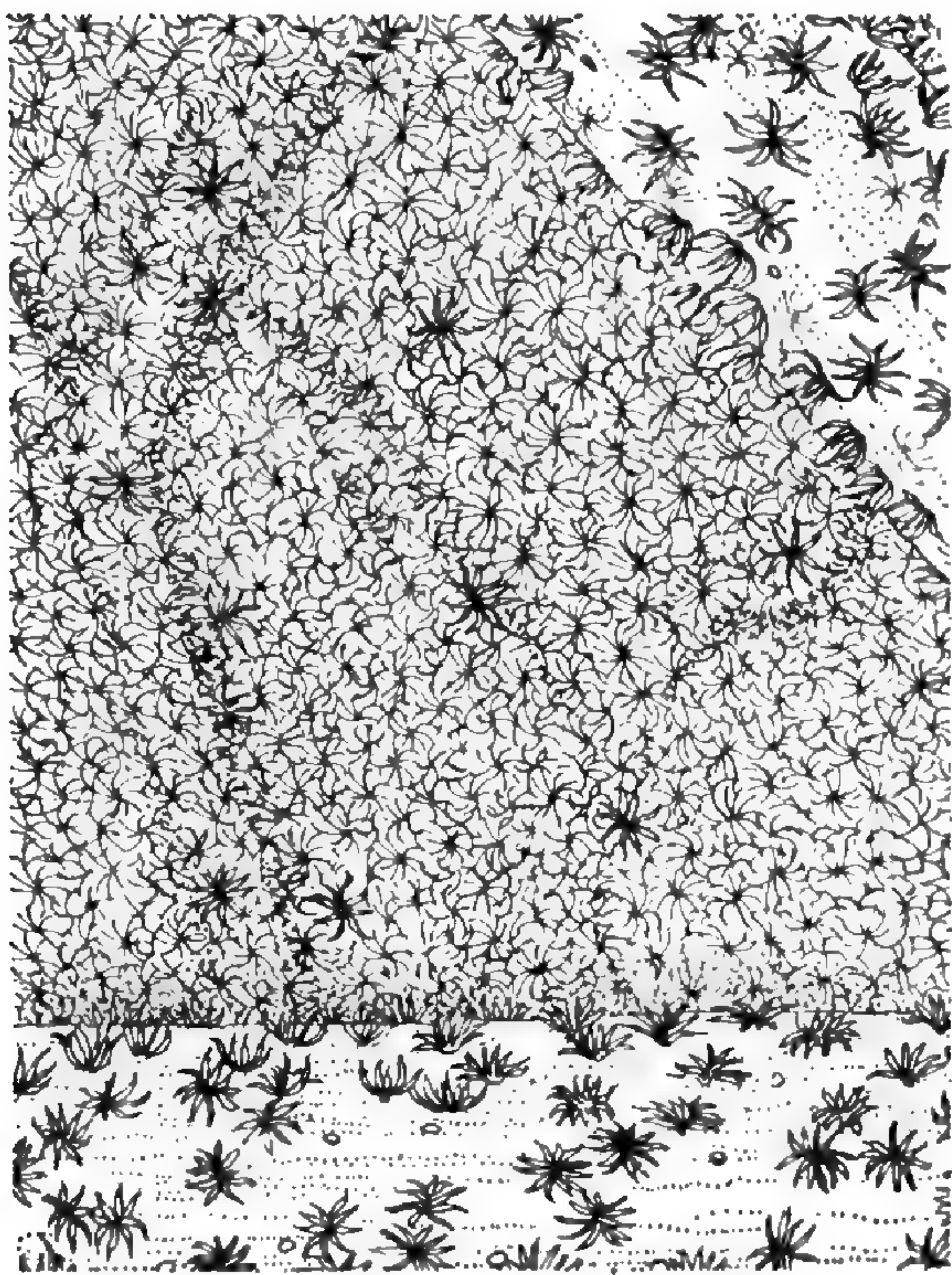
PUTUMAYO: Río Caucayá, Laguna Primavera on Río Leguízamo; tree 18 m., symmetrical jorquette, 3 IV 1953, *Holliday & Cope* T/91 (COL, TRIN, US).



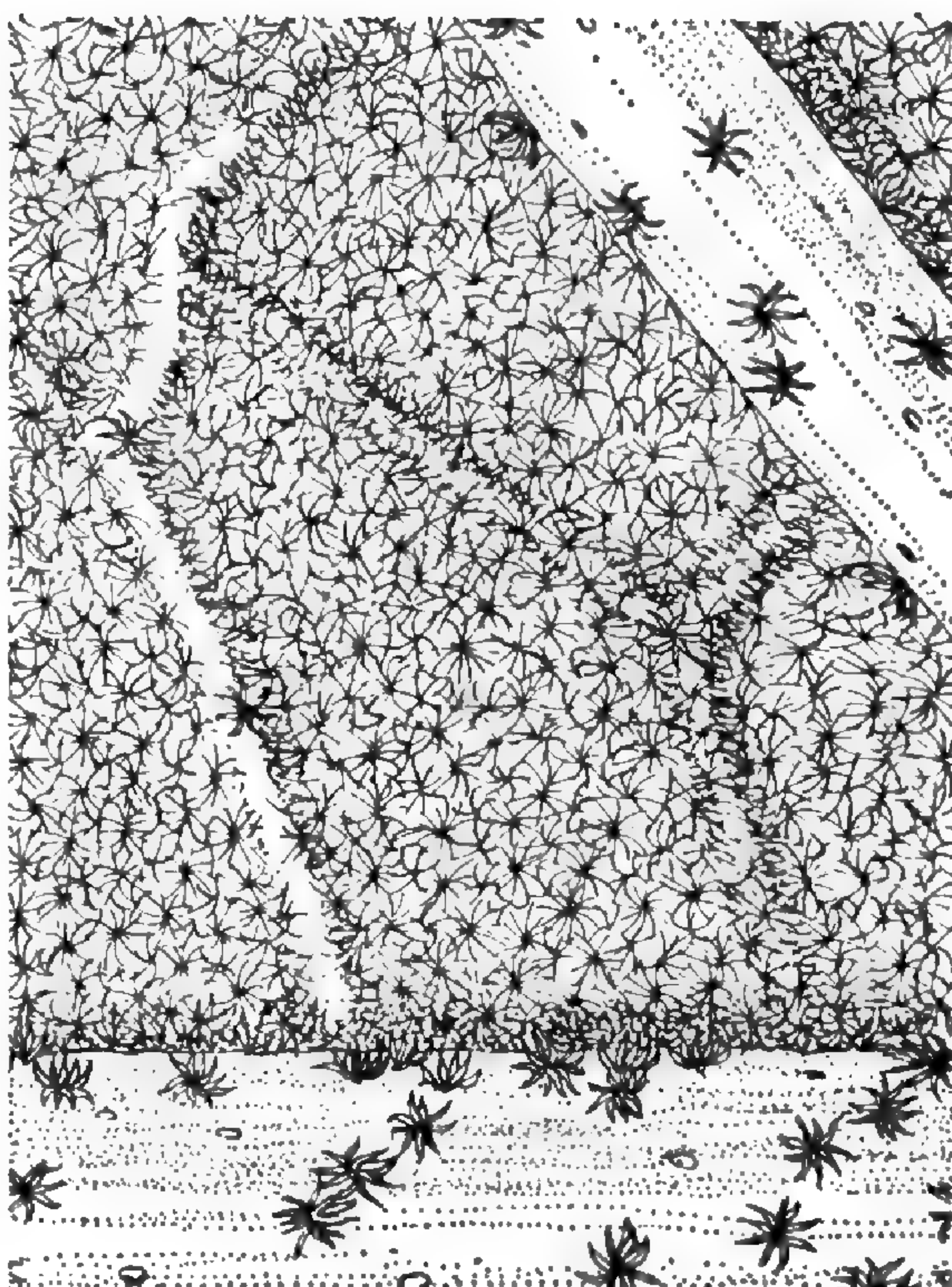
A



B



C



D

FIGURE 41.—Detail of indument on the underside of leaf in: A, *Theobroma subincanum* (Cuatr. 7277); B, *T. sinuosum* (Pavon, s.n.); C, *T. nemorale* (Cuatr. 21921); D, *T. mammosum* (Leon 1363). A, C, and D $\times 25$, B $\times 10$.

Vicinity of Mocoa; tree in forest, 15 m. high, no fruits or flowers, 17 III 1953, Holliday & Cope T/81 (COL, TRIN, US).

CAQUETÁ: Río Caguán, camp 4; tree 10 m., 26 IV 1953, *Holliday & Cope* T/116 (COL, TRIN, US). Upper Río Caguán; small trees, 10 IV 1953, *Holliday & Cope* T/101 (COL, TRIN, US), 13 IV 1953, *Holliday & Cope* T/103 (COL, TRIN, US). Solana, 8 km. SE. of Tres Esquinas, on Río Caquetá, below mouth of Río Orteguaza, 200 m. alt., wet tropical forest; tree 15 m. high, 15 cm. thick, bark gray, smooth, with lichen patches and bryophyte patches, long, ellipsoidal orange-brown fruits 10 x 6–6.5 cm., edible, "cacao silvestre," 4 VI 1945, *Little & Little* 9544 (F, US) (fruit US No. 1096). Municipality of Florencia, site San Luis, right margin of Pescado River, "cacao silvestre" 5 VI 1942, *Ranghel* 195 (in part) (COL).

VAUPÉS: Caño Mayabo, near San Felipe, river level; only flowers and old fruits, no young or ripe fruit at this season, 27 X 1952, *Baker* 33 (COL, F, TRIN, US). Mitú: Caño Paraná-Midí, 200 m. alt.; tree 5 m., 19 X 1939, *Cuatrecasas* 7277 (F, US, COL). Cerro de Mitú, 380 m. alt.; small tree with bending, fruiting branches, fruits 9.3×6 cm., 17 IX 1939, *Cuatrecasas* 6890 (COL, F, US). Mitú and vicinity, 280 m. alt.; tree, cultivated, 22–30 VI 1958, *García Barriga, Schultes & Blohm* 16064 (COL). Ibidem; tree 5 m. with spreading branches, flowers red, 10–13 XI 1952, *García Barriga* 15139 (COL). Cerro de Circasia, 300 m. alt., base of hill 10 X 1939, fruiting tree, 10 X 1939, *Cuatrecasas* 7178A (COL, F, US). Río Barbas, river level, native in the forest, 28 X 1952, *Holliday* 43 (COL, F, TRIN, US). Río Cuduyarí, tributary of Río Vaupés, Yacara, middle and lower course, highland, ± 700 –800 feet, 9 XI 1952, *Schultes, Baker, & Cabrera* 18552 (US). Río Cuduyarí, river level, showing jorquette of 3 branches, 16 X 1952, *Baker & Cope* 31 (F). Ibidem; young red flowers, *Baker, Bartley, & Holliday* 31 (COL, TRIN). Río Cuduyarí, Pakwativa Mission, river level, heavily infested with *Marasmius perniciosus*, 19 X 1952, *Baker & Cope* 32 (COL, F, TRIN, US). Ibidem; flowers distinctly paler in color, *Baker, Bartley, & Holliday* 32a (TRIN). Río Apaporis, Soratama, above mouth of Río Cananarí, Caño Surrucó, 900 feet alt., highland; small tree, leaves rusty beneath, fruit rusty brown, ovoid, 30 I 1952, *Schultes & Cabrera* 15116 (US). Río Apaporis, Río Jinogojé, river level; tree 40–50 ft., native in forest or river bank, 13 IX 1952, *Baker & Cope* 12 (TRIN). Jinogojé, growing just above flood level with numerous ellipsoid pods, *Baker & Cope* 7 (COL, TRIN). Ibidem; river level, tree 16 m., 20 cm. diam. at base, a long, tall thin pole, without obvious jorquettes, native in forest, 23 VIII 1952, *Baker & Cope* 3 (COL, F, TRIN, US). Ibidem, 250 m. alt.; tree 15 m., large, coriaceous leaves, brownish fruits 7.5×4.5 cm., 25, 26 VIII 1952, *García-Barriga* 14224 (COL, US). Río Piraparaná, cultivated tree, 21 VIII 1952, *Schultes & I. Cabrera* 17005 (AMES). Río Piraparaná, 250 m. alt.; tree 3 m., red petals, sepals red above, 22–26 VIII 1952, *García-Barriga* 14203 (COL, US), 14253 (COL). Río Piraparaná, near confluence with Río Apaporis, river level; small tree 3 m., in Indian garden, 24 VIII 1952, *Baker & Cope* 4 (COL, F, TRIN, US). Río Inírida, near Morichal, near the mouth of Río Papunaná, 200 m. alt.; tree 10 m., 14 II 1953, *Fernández* 2275 (COL, US). Río Inírida, Raudal, 300 m. alt., 3 II 1953, *Bartley & Holliday* T/71 (COL, TRIN, U, US). Río Inírida, Santa Rosa; tree 12 m., 25 I 1953, *Bartley & Holliday* T/68 (COL, TRIN, U, US). Río Inírida, right bank below Caño Caribe (5 hours above Morichal); tree about 10 m., no flowers, one small fruit, 22 I 1953, *Bartley & Holliday* T/65 (COL, E, TRIN). Río Inírida, Morichal, 30 m. alt., in forest, small fruits, no flowers now, 8 II 1953, *Bartley & Holliday* T/72 (COL, TRIN, US). Río Inírida, affluent Papunaná, 300 m., red leaf flush, nearly mature pod 11.5×6 cm., fruit pedicel 2 cm. long, fruit green with brown pubescence, pericarp woody, pulp white, cotyledons white, convolute, 18 II 1953, *Bartley & Holliday* T/75 (COL, TRIN, US).

AMAZONAS: Río Caquetá, La Pedrera, river level; tree 45–50 ft., native in forest, 29 IX 1952, *Baker & Cope* 25 (COL, F, TRIN, US). La Pedrera, river level, native tree in forest, 26 IX 1952, *Baker & Cope* 21 (TRIN). Río Caquetá, Remolino, leaves from young tree, 2 V 1953, *Holliday & Cope* T/124 (COL, TRIN, US). Río Apaporis, near mouth of Río Cananarí; tree 45 feet tall in forest, fruit rust colored, “cacao de monte,” III 1951, *Schultes* 12104 (COL, US). Río Apaporis, between Río Pacoa and Río Cananarí, Soratama, 250 m. alt.; weak tree, leaves rusty beneath, flowers red, 26 IX 1951, *Schultes & Cabrera* 14140 (US). Río Miritiparaná, near varadero to Río Apaporis, river level; tree 50 ft., native in forest, 15 IX 1952, *Baker & Cope* 13 (COL, TRIN). Trapecio Amazónico, Loretoyacu River, 100 m. alt., IX 1946, *Schultes* 8385 (AMES, F). Leticia, 100 m. alt.; bark rough, cracked, light gray, flowers red, 20 IX 1945, *Schultes* 6536 (F). Leticia, forest; flowers pale red, tree 5 m., 22 VIII 1946, *Black & Schultes* 46–61 (USDA).

VENEZUELA: BOLIVAR: Mount Duida, 500 m. alt.; small tree, VIII 1928–IV 1929, *Tate* 944 (NY, US). Caroní, rain forests of the Icaburu valley, 440 m. alt.; tree 15 m., fruit large and tasty, “padamá” (Arekuna), XI 1947, *Cardona* 2379 (US, VEN).

AMAZONAS: Alto Río Orinoco, Tamaná, 121 m. alt.; medium-sized tree (10–12 m.) with few branches, flowers purplish or red on the branchlets, trunk bent, up to 40 cm. diam. with no branches in 2–5 m., bark gray, inside light brown, wood pale brownish; “cacao-rana,” *Ll. Williams* 15204 (A, F, G, US, VEN). Río Guainía, Maroa, river level, with one ripe pod (wall mealy, smooth, thin and brittle), seeds extracted and sent to Trinidad, *Baker* 38 (COL, F, TRIN, US).

FRENCH GUIANA: *Aublet* s.n. (part of syntype of *Cacao guianensis* Aublet, BM, Photo, Mo. Bot. Gard. no. 4028). “Guyane Francaise,” *Poiteau*, s.n. 1819–1821 (G). French Guiana, “*Cacao sylvestris* Aublet,” *Aublet* (syntype, BM, Photo Mo. Bot. Gard. no. 4029).

BRAZIL: AMAZONAS: Rio Negro, Barcellos, “cupuhy,” 25 VI 1905, *Ducke* 7200 (MG). Rio Negro, Rio Caure, Igarapé Mirití; tree 5 m., 15 cm. diam., red flowers, in rather lowland high forest, VII 1948, *Fróes* 23343 (IAN, P). Rio Negro, Porto Cabary, “cupuhy,” 4 XII 1945, *Fróes* 21482 (IAN, NY, USDA). “Prov. Rio Negro Martius Iter. Brasilienses 325,” *Martius* [898] (M) (Photo F. M. 19645). “Prov. Rio Negro, Martius Iter. Bras. 325,” *Martius* [872, 873 p. p., 894, 895, 896, 897, 899, 900] (M). “Rio Negro Dr. Martius Iter Brasil. 325, *Theobroma subincanum*,” *Martius* [893] (M) (Photo F. M. 40704). Rio Vaupés: Jauraté, inundatable forest, 17 X 1945, *Fróes* 21162 (IAN, NY, USDA). San Antonio de Iça, forest; tree 10 m. “differt a *T. ferrugineo* Bern. foliis majoribus latioribus floribus majoribus,” *Ducke* 7679 (MG, F) (Photo F. M. 7679). Municipality of São Paulo de Olivença, near Palmares; tree 40 ft. high, trunk 5 inches diam., high land, “cupuarana,” 11 IX–26 X 1936, *Krukoff* 8226 (A, BM, F, G, GB, K, LE, MO, NY, P, U, US). Basin of Rio Madeira, Municipality Humayta, near Livramento, on Rio Livramento, terra firma; tree 60 ft. high, “cupuarana,” 12 X–6 XI 1934, *Krukoff* 7016 (A, F, G, K, MICH, MO, S, U, US, WU). Rio Madeira, Varadouro do Morcego, 31 VIII 23, *Kuhlman* 18110 (U). Manaus, mata; arvore, tree 30 m. alt., 15 cm. diam., “cupuhy,” 17 II 1945, *Fróes* 20518 (IAN, K, NY, USDA). Manaus, Mata do Aleixo, “cupuhy,” 16 III 1945, *Fróes* 20555 (F, IAN, USDA). Manaus Aurora Fazenda, 15 m., Urwald, “cupú do Matto,” 28 VIII 1921, *von Luetzelburg* 22079 (M). Without locality *Spruce* 97 (K).

AMAPÁ: Rio Amaparí, Serra do Navio, slopes of Curuca Ore Body, down to Igarape Sentinela; occasional tree 6 m. tall; fruit brown, 9 XI 1954, *Cowan* 38186 (NY, US). Lower slopes of Observatorio Ore Body, heavily forested hills,

70–300 m. alt.; tree 10 m. tall, fruit brown, 8 XI 1954, *Cowan* 38164 (NY). Missao do Servico Florestal no T. Amapá, IX 1955, *Miranda Bastos* 68 (IAN).

PARÁ: Belém, "cupuahy," VI 1896, *Huber* 162 (BM, G, MG, P, (US). Belém, Bosques Rodriguez Alves, 1 VIII 1944, *A. Silva* 317 (IAN, USDA). Belém, Horto do Museo Goeldi; tree 481, small tree, flowers brown yellow, 22 XII 1958, *Cavalcante* 938 (MG, US). Belém, Bosque municipal; tree 30 feet high, sparsely branched, 4 VIII 1942, *Archer* 7517 (IAN, USDA). Belém, south forest of the Instituto Agronómico do Norte; large tree, contents of fruit eaten by birds, "cupu-assuy," 16 XI 1942, *Archer* 7820 (IAN, USDA). Belém, along roads on lands of Inst. Agr. do Norte; large tree, flowers rose color, "cupu-assu-rana," *A. Silva* 237 (IAN). E. F. Bragança, João Coelho; tree 8 m., 14 III 1947, *Pires & Black* 1414 (IAN). Region of Igarapé Pitoró; tree 10 m., flowers red, 19 IX 1958, *Fróes* 34663 (IAN). Taperinha, near Santarém, bushed river margins of Igarapé Assú, "cupuy do Igapó," 23 VIII 1927, *Ginzberger & Hagmann* 801 (F, WU). Rio Tapajóz, Cachoeira do Mangabal, "beira de assahyzal," "cupuy," 6 IX 1916, *Ducke* 16464 (BM, MG). Matta do Alto Ariramba, "cupuy" 7 X 1913, *Ducke* 14925 (MG). Rio Purús, Monte Verde, "cupuahy," II 1904, *Goeldi* 4225 (MG). Paranary, upper Amazon, "cupua-i," 20 X 1874, *Traill* 59 (K, P).

GUAPORÉ: Porto Velho, km. 8, in high forest on firm land; tree about 30 m., "cupuí," 17 VI 1952, *J. F. Silva* 143 (IAN).

RIO DE JANEIRO: Quinta de S. Christovao; small tree planted by Riedel probably originally from Amazon basin, "cupuaí," 16 II 1876, *Glaziou* 9633a (P).

PERU: LORETO: Mishuyaco, near Iquitos, 100 m. alt., forest; tree 6 m. high, flowers dark red, "wild cacao," X–IX 1929, *Klug* 87 (F, NY, US). Ibidem, II–III 1930; tree 8 m. high, flowers wine red on branches, *Klug* 857 (F, US). Alto Itaya, 145 m., in forest of Paraíso, "cumalá," 30 IX 1929, *Ll. Williams* 3254 (A, F, G, S, US). Upper Río Nanay, Santa Ana, "uchpa-cacao," 7 VII 1929, *Ll. Williams* 1233 (F, S, US). Río Nanay, Tierra Doble, deep forest, "Campamento balatero Lira Dabu," 8 VI 1929, *Ll. Williams* 1076 (US, F, S). "Peru," *Ruíz & Pavón*, "Theobroma alba R. & P." (ined.), "*Theobroma ferruginea* Bern." (K, BM). Ibidem, *Herb. Pavón* 201 (G). "*Theobroma alba*," *Rivero* 1836 (P). *Tessmann*, s.n., NY–3717; probably the same as the *Tessmann* 4115, cited by *Mildbraed* (Notizbl. 11:139. 1931) as *T. ferrugineum* and collected near Pongo de Manseriche, 160 m. alt., tree 19 m. tall, 21 cm. diam., "pako-kakao" (Dunkel Kakao), 23 IX 1924.

HUÁNUCO: Prov. Huánuco, Tingo-María, forest, tree about 25 m. high, sepals olivaceous yellow without, more or less red within, petals yellowish gray, 31 VIII 1940 *Asplund* 13410 (S). Tingo María, forest; tree 15 m., flowers dark red, 8 VIII 1940, *Asplund* 12911 (S). Maynas, Yurimaguas, "yurac-cacao" i.e., "Cacao album Peruvianum," March, 1831, *Poeppig* 2352 p.p. (GH, P, WU).

TRINIDAD (cultivated): On grounds of the I.C.T.A., from seeds from Mitú Vaupés region, Colombia; one branch damaged by *Marasmius perniciosus*. *Cuatrecasas, Cope, & Bartley* 25785 T (U.S.)

18. *Theobroma hylaeum* Cuatr., sp. nov.

FIGURES 25, 39; MAP 11

Arbor circa 10 m. alta, apicaliter crescens, ramis primariis ternatis, ramulis brunneis juvenilibus minute ferrugineo-tomentosis denique glabratis, cortice rugoso-fissurato; stipulae lineari-subulatae acutae vel subacutae ferrugineo-tomentosae, circa 6 mm. longae, 1 mm. latae.

Folia mediocriter coriacea, petiolo crassiusculo subtereti minute ferrugineo-tomentoso, 6–10 mm. longo; lamina elliptico-oblonga vel obovato-oblonga, basi symmetrica attenuata obtusa vel subobtusa, apice leviter attenuata interdum rotundata subite acuteque acuminata, margine integra vel apicem versus leviter undulata, 12–20 cm. longa, 4–9 cm. lata, apiculo 6–15 mm. longo, supra in sicco viridibrunnescens glabra, costa et nervis principalibus filiformi-impressis reliquis vix conspicuis, subtus cinereo-ochracea vel nervatione ferruginea, areolis venulisque cinereo-tomentosis pilis stellatis minutis albidis intricatis dense tectis et pilis stellatis crassioribus ferrugineis sparsis vel in nervis copiosis, costa crassa elevata, nervis secundariis 7 vel 8 utroque latere eminentibus arcuato-ascendentibus, prope marginem tenuioribus anastomosantibus, nervis tertiariis transversis prominentibus, nervulis venulisque tenuioribus sed prominulis reticulatis.

Inflorescentiae breves axillares cymis 1–3 floribus instructae, ramulis brevissimis tomentosis, pedunculis tenuibus erectis vel subflexuosis ad 12 mm. longis ferrugineo-tomentosis apice 3-bracetolatis et cum pedicello articulatis; bracteolae anguste lineares subacutae, 3–6 mm. longae, 1–2 mm. latae, extus tomentosae; pedicelli erecti tomentosi pedunculis leviter crassiores, 5–6 mm. longi.

Sepala crassiuscula ovato-oblonga acuta, basi ad 2 mm. coalita, patulo-reflexa, extus ochraceo-tomentosa, intus margine minutissime albido-tomentella excepta glabra, aurantiaca, basi ad insertionem pilis crassiusculis oblongis glandulosis annulum formantibus, 8–9 mm. longa, 4–5 mm. lata; petala cucullo aurantiaco obovoideo, basi angustato, apice rotundato, saccato-cucullato, 3 mm. longo, 2 mm. lato, extus glabro ruguloso, intus minute hispidulo, 7-nervato, pediculo 2.5 mm. longo, parce puberulo, lamina obovato-subrhomboidea crassa brunneo-rubra, faciebus sparsis minutissimis pilis margine pilis flexuosis tenuibus praedita, 4–5 mm. longa, circa 4 mm. lata; androecium tubo circa 1.5 mm. longo; staminodia petaloidea aestivatione reflexa in anthesin curvato-patula, brunneo-rubra obovato-oblonga apice rotundata vel leviter retusa, 5–5.5 mm. longa, 2.2 mm. lata, minute pilosula; filamenta fertilia 1 mm. longa; antherae 3. brevissime pedicellatae; ovarium obovatum 1.2 mm. longum, 1 mm. latum, crasse tomentosum; styli circa 1 mm. longi coaliti.

Fructus coriaceus circa 7 x 4 cm., viridi-brunnescens, adpresse tomentosus laevis ellipsoideus, utrinque rotundatus, epicarpio rigido lignoso in sicco 1 mm. crasso; pedunculus fructifer 1.5–1.8 cm. longus, 0.8 cm. crassus.

Type in the U.S. National Herbarium, No. 2028683, collected in the heavy rain forest around Villa Arteaga, northern region of An-

tioquia, Colombia, at 200 meters altitude, August 14, 1948, by J. Araque and F. A. Barkley no. 18C745.

COMMON NAMES.—Chocolate de monte, cacao silvestre.

DISTRIBUTION.—Presently known only from the Chocó region of northern Antioquia, Colombia, and probably also in Panama.

COLOMBIA: ANTIOQUIA: Villa Arteaga, heavy wet forests at 200 m. alt.; tree 10 m., flowers orange, corona cream orange, stigma black brown, 14 VIII 1948, *Araque & Barkley* 18C745 (holotype, US 2,028,683; isotype, US 2,028,684, COL). Ibidem; seedlings showing symmetrical branching in 3's, growth continuing from above the jorquette, 24 VII 1953, *Bartley & Holliday* T 166 (K, TRIN, US).

PANAMÁ: COLÓN: Along Río Fató, in forests or thickets 10–100 m. alt., VII 1911, *Pittier* 4194 (BM, GH, US) (probably; specimen sterile; identification needs confirmation by fertile specimens).

Theobroma hylaeum is closely related to *T. nemorale* from which it differs essentially by the narrow-linear bracts and stipules, by the subrhomboid lamina, and by the narrower obovate-oblong, rounded and notched staminodia; furthermore, the peduncles and the pedicels are short, the pedicels shorter than the peduncles, and the fruit is harder, smaller and not constricted above the base. From *T. subincanum* it differs by the shape of the petal-laminae and staminodes, by the tomentose ovary, by the smaller fruit and leaves, and by the venation, in which the minor veins are less conspicuous.

19. *Theobroma nemorale* Cuatr.

FIGURES 3, 41, 42; MAP 11

Theobroma nemorale Cuatr., Rev. Acad. Colomb. Cienc. 8:487, fig. 4. 1952; Baker, Cope, & al. (1954) 13, fig. 20; León (1960) 323, fig. in 321.

TYPE.—Pacific coast, Colombia, *Cuatrecasas* 21291 (fruiting specimen), *Patiño* 24 (flowering specimen, paratype).

Small or medium-sized tree up to 15 m. high; growth pseudoapical; trunk up to 20 cm. in diameter; primary branches ternate; leafy branches ochraceous or ochraceous-ferruginous, or brownish, minutely and appressed tomentose, the older glabrate, dark grayish, rather smooth or granulate-lenticellate, nitidous, the hornotinous greenish ferruginous, tomentose; stipules subcoriaceous, oblong, obtuse, striolate, tomentose, about 8–11 mm. long, 2–3 mm. broad.

Leaves coriaceous, moderately rigid; petiole 9–12 mm. long, thick, subterete, densely and appressed ferruginous-tomentose; blades elliptic-oblong or obovate-elliptic-oblong, slightly attenuate and asymmetrical, or equilateral, rounded at base, rounded or obtuse and abruptly acuminate at apex, entire or upwardly sinuate or coarsely dentate, 10–32 cm. long, 3–12 cm. broad, the acute acumen 1.5–2.5 cm. long, above green, pale brown when dry, rather shining, glabrous, the costa depressed, thin, the other nerves rather inconspicuous, cinereous or greenish cinereous beneath, or pale tawny when dry, the costa very prominent, the secondary nerves about 8 on each side very

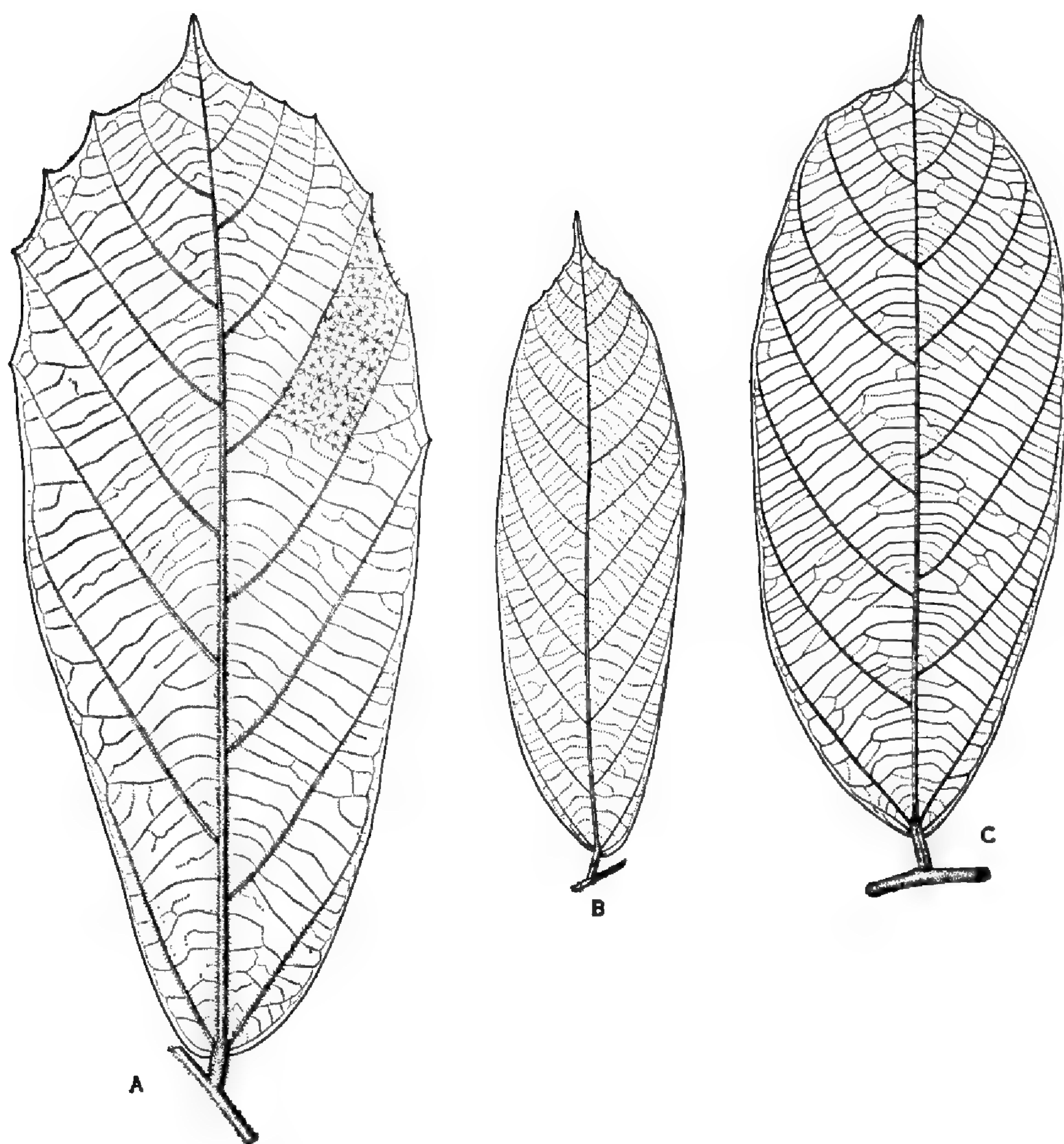


FIGURE 42.—Leaves of *Theobroma*, $\times \frac{1}{2}$: A, *sinuosum* (Pavon, s.n.); B, *mammosum* (Leon 1363); c, *nemorale* (Cuatr. 21291).

prominent, subparallel, ascending, curving and anastomosing near the margin, the transverse tertiary nerves prominent, parallel, the nerves of the fourth rank prominulous, broadly reticulate, the minor reticulate veins concealed, the whole nervation tomentose, greenish ochraceous or subferruginous, by rather thick, tawny, densely distributed stellate hairs, the surface within the veins covered by a dense and appressed cinereous tomentum of white, fine, minute stellate hairs.

Inflorescences axillary or on exfoliated branchlets very small, reduced to 1–3 (–5) flowers, the cyme-axis extremely short, the peduncles 5–10 mm. long, erect, ferruginous-tomentose, 3-bracteolate at apex, the pedicels thicker, ochraceous-ferruginous tomentose, 2–5 mm. long, the bracts ovate, obtuse, 2.5–3 mm. long, 1.5–2 mm. wide; bracteoles 3, broadly cochlear, embracing the bud, orbicular or ovate-rounded,

ochraceous-greenish tomentose, 7–11 mm. long and broad, soon caducous.

Sepals thick, ovate-oblong, subacute or subobtuse, 9–10 mm. long, 4–5 mm. broad, united in the lower third or fourth, first curved-patulous, later reflexed, inside purplish or rose, shining, glabrous except for the minutely white-tomentose margin, and for the minute oblong-capitate, glandular hairs at the base, thick-tomentose outside, ochraceous, the stellate hairs with long, thin rays.

Petal-hoods thick-membranaceous, ochraceous or orange, obovate with rounded-cucullate apex, 7-nerved, glabrous and rugose outside, minutely hispidulous-pubescent, inside with 7 prominent veins, 3–3.5 mm. long, 2–3 mm. broad; petal-lamina pedicellate, carnose, rigid, red or crimson becoming brownish red, oblong-obovate-spatulate, rounded or subtruncate-emarginate at apex, with very minute, sparse hairs on the surface and copious longer, slender, weak, spreading hairs on the margins, 5–7 mm. long, 3–5 mm. broad; pedicel narrowly linear, folded, puberulous, at the broader base barbate, 3 mm. long; androecium tube 1.5–2 mm. long; staminodes laminar, rather thick, obovate-oblong, rounded or subspatulate at apex, purplish red or crimson, covered with sparse, thin, minute hairs, 6–7.5 mm. long, 3.5–4.5 mm. broad, reflexed in bud, spreading in anthesis; filaments moderately thick, 1–1.2 mm. long, pilose towards the base, 3-furcate (the branchlets 0.4 mm. long), 3-antheriferous, the anther lobes ellipsoid 0.5–0.6 mm. long, connivent; ovary 1.3–1.5 mm. long, oblong-ovoid, subtruncate, 5-ridged, thickly ochraceous, hirsute-tomentose; styles linear, glabrous, 1.5 mm. long, coherent.

Fruit ellipsoid, smooth, rounded at apex, slightly constricted above the base, 8–10 cm. long, 4.5–6 cm. broad; pericarp coriaceous, rigid, 1–1.5 mm. thick, when mature fragile, its surface densely appressed stellate-tomentose, greenish or bluish, at maturity yellowish, brown or tawny; seeds compressed ovoid or subellipsoid, 17–19 mm. long, 9–12 mm. broad, the surrounding pulp white, yellowish when ripe; cotyledons white; fruiting peduncle robust, 1.5–2 cm. long, about 0.8 mm. thick; germination hypogeous.

COMMON NAMES.—“Bacao de monte,” “chocolate de monte,” “bacao,” “bacaíto,” “cacao de monte,” “cacaíto de monte.”

USES.—It is said to produce a fairly good chocolate; not known to be used by the natives.

DISTRIBUTION.—Restricted to the Colombian Pacific coast and the Chocó area between the parallels 3° and 5°3' N. latitude. It is recorded from the Calima, San Juan, and Cajambre Rivers.

This very interesting species is closely related to *T. subincanum* and *T. hylaeum*, but it differs specially by its three broad, orbicular bracteoles subtending the flowers, which before anthesis embrace

and cover the short-pedicellate bud. This feature is unique in the genus *Theobroma*.

The leaves of *T. nemorale*, as well as those of *T. hylaeum*, are very similar to those of *T. angustifolium*, but they are broader, more oblong-elliptic, with a tendency to an obovate shape, and the ochraceous or ferruginous hairs beneath are smaller, with shorter, somewhat thicker rays than in *T. angustifolium*.

COLOMBIA: Chocó: Río San Juan, Palestina; part of branch brought in by an Indian, one immature fruit 7 x 4.5 cm., 4 VIII 1953, *Holliday* T/149 (TRIN, US). Ibidem, young tree 3 m., sterile, 2 VII 1953, *Holliday* T/147 (TRIN, US). Ibidem, sucker 1½ m. from leafless fallen trunk, 2 VII 1953, *Holliday* T 148 (TRIN). Ibidem, Quebrada de las Sierpes; tree 10 m. tall, leaves green yellowish above, ashy beneath, 24 IX 1961, *Cuatrecasas & Willard* 26051 (COL, US). Istmina, tree about 7 m., sterile, flowers apparently borne only on branches, 2 VIII 1953, *Holliday & Bartley* T/173 (TRIN, US).

EL VALLE: Pacific Coast, Río Calima, La Trojita, 5–50 m. alt.; small tree; leaves coriaceous yellowish green, fruit ovoid-ellipsoid, 8 x 4.5 cm., light brown, "bacao de monte," 28 II 1944, *Cuatrecasas* 16544 (F, VALLE). Río Calima, Quebrada de la Brea, 20–40 m. alt.; tree 8 m., leaves subcoriaceous, medium green above, green cinereous beneath, nerves green ochraceous, fruits 10 x 6 cm., ellipsoid, rounded at apex, constricted at base, tawny, on the branchlets, "chocolate de monte," 24 V 1946, *Cuatrecasas* 21291 (holotype, F; isotypes, B, F, VALLE). Ibidem, La Brea, flowering specimens, *Patiño* 24 (paratype, F; type of flowers; isoparatypes, F, US). Estación Agroforestal del Calima, 30–50 m. alt.; erect tree with abundant hanging pods, 8 I 1953, *Patiño* 117 (US, Herb. Cuatr.). Ibidem; small tree 8–10 m., "cacao," "cacaño de monte," "bacaño," 8 I 1953, *Patiño* 116 (US, Herb. Cuatr.). Ibidem; tree with primary ternate branches from near the ground; leaves light green; twigs tomentose ochraceous or ferruginous, sepals thick, rose or purplish rose inside, ochraceous outside, petal-laminae and staminodes thick, rigid, purplish red or dark brown red, hoods ochraceous with 7 red veins, "bacao," 23 IX 61, *Cuatrecasas & Willard* 26007 (COL, US). Caño La Brea; young tree 1.5 m., sterile, 29 VI 1953, *Holliday* T/141 (TRIN, US). Estación Agroforestal; tree 8–10 m., in land cleared from forest, jorquette symmetrical, crimson and yellow flowers borne singly or in pairs on small branches, pods 8.5–10 x 5–5.5 cm., fruit peduncle 2 cm. long, 0.75 cm. thick, 29 VI 1953, *Holliday* T/146 (TRIN, US). Pacific coast, Río Cajambre, Silva, Loma de la Vigia, 5–80 m. alt.; small tree, leaves green above, gray beneath, "bacao de monte," II–V 1944, *Cuatrecasas* 17503 (F, VALLE). Ibidem, Quebrada del Corosal 0–5 m. alt.; tree 15 m. tall, trunk 20 cm. diameter, leaves coriaceous, green above, ashy beneath, fruits ellipsoid rounded at apex, contracted above the base, smooth, brownish, 10 x 5.5 cm., "chocolate de monte," 17 V 1944, *Cuatrecasas* 17738 (F, VALLE).

TRINIDAD (cult.): Imperial College of Tropical Agriculture, River State Diego Martínez, Field 19; 7–8 years old tree, 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25782 T (US).

20. *Theobroma sinuosum* Pavón ex Huber FIGURES 41, 42; MAP 9; PLATE 12
Theobroma sinuosum Pavón ex Huber, Bull. Herb. Boiss., II, 6:274. 1906.
Theobroma Tessmannii Mildbr. Notizbl. Bot. Gard. Berlin 11:139. 1931.
Theobroma sinuata Ruiz & Pavón, Fl. Peruv. et Chil. Fol. E, Plate 417, ined.

Types.—Chicoplaya, Peru, *Ruíz & Pavón* (lectotype, G). Marañón River, Peru, *Tessmann* 4928 (type of *T. tessmannii*).

Large tree with erect trunk; leafy terminal branchlets brownish ochraceous when dry, densely hirsute-tomentose, covered by minute, whitish, stellate hairs with intricate, slender rays (0.1–0.2 mm. long) and by larger stellate, ferruginous hairs with straight, acute, long rays (1 mm. long); stipules lanceolate, about 1 cm. long, deciduous.

Leaves subcoriaceous, firm; petiole short, thick, densely tomentose-hirsute, about 1 cm. long; blades obovate-oblong, slightly attenuate, rounded and slightly asymmetrical and emarginate at base, subrounded and abruptly triangular-cuspidate at apex, sinuate-dentate in upper third, otherwise entire, about 30 cm. long, 13 cm. broad, pale green brownish above, when adult glabrous with abundant reddish, punctiform scars, the midrib and secondary nerves filiform impressed, the other nerves less visible, softly tomentose beneath, subochraceous, covered by a dense, cinereous layer of minute, white, fine, stellate hairs and, especially on nerves, by larger ochraceous, stellate hairs, with 4–6, erect, acute, rays 1–1.5 mm. long; the midrib thick, prominent, densely tomentose-hirsute, the secondary nerves about 9 on each side, ascending, prominent, vanishing near the margin, hirsute, the tertiary, transverse nerves prominent, parallel, 5–10 mm. distant from each other, the minor veins reticulate and prominulous.

Sepals ovate-lanceolate united at base, reflexed; petal-hoods obovate, concave; petal-lamina obcordate-“trigonus”; staminodes lanceolate-obovate; stamens five, 3-antheriferous; ovary hirsute; fruit subrounded-pyriform, the epicarp smooth, hard, woody, ferruginous tomentose.

The preserved original specimens from the Ruíz and Pavón herbarium surely collected by Tafalla have only leaves; they have been used by me for the above description. The short description of flowering characters has been taken from the manuscript of the unpublished Flora of Peru and Chile of Ruíz and Pavón. This description was written by Ruíz or Pavón based on data sent by Tafalla. Some of the data were misinterpreted by the authors who describe the anthers “quinque in singulo filamento,” and this is not the case. Tafalla wrote in his “notas” that each filament was divided in six “lacinias” bearing one anther each, and that the number of stamens was five in *T. alba*, *sinuata*, and *cordata*, whereas it was ten in *T. digitata*. Pavón described the inflorescences as being cauline; we have no basis either to affirm or deny that assertion. The petal-lamina is described as “trigona”; probably it was slightly 3-dentate, and this feature was extremely exaggerated by Pulgar in his drawing.

Theobroma sinuosum, because of the little information available, was disregarded by most of the authors who listed cacao species; Chevalier

who saw specimens of it considered it as a synonym of *T. ferrugineum*, which was not well defined by him in his revision. My study of the sterile specimens of the type convinces me that *T. sinuosum* is a very different species, unique in possessing an indument comparable to that of the young plants of *T. chocoense* and *T. simiarum*. On the other hand, after careful study of the description and photograph of *T. tessmannii* Mildbr. which I had formerly associated with *T. subincanum*, I arrived at the conclusion that the Tessmann specimen is definitely distinct from *T. subincanum* and that it coincides with *T. sinuosum*. Unfortunately the Tessmann specimens are not existing any more, but the Mildbraed's detailed description of the indument permits us to differentiate his species from the closest allied species growing in the same area, namely *T. subincanum*. Some doubts may remain about the identity of *T. sinuosum* and *T. tessmannii*. The Tessmann plant definitely had axillary inflorescences, whereas the Pavón plant was described as being cauliflorous, but the species could well have both cauline and axillary inflorescences. The geographical range and the identical kind of indument are the reasons that I consider the species synonymous.

I wish to supplement the description given above with the data taken from Mildbraed's description: Leaves subcordate at base, 25–35 cm. long, 8–12 cm. broad, with about 10 secondary nerves; sepals lanceolate, acute, about 10 x 4 mm., connate at base for 2 mm.; petal-hood whitish, lamina red, subquadrate-rounded and apiculate, 3 x 3 or 2 x 3 mm.; staminodes dark red, subspatulate-elliptic, 6 mm. long, 3 mm. broad; stamens 3-antheriferous; pedicels 2 cm. long.

COMMON NAMES.—Cacao de monte, Pako Kakao (*Tessmann*).

USES: The pulp of the fruits is eaten by the natives.

DISTRIBUTION.—Upper river valleys of the Huallaga and Marañón in Peru.

PERU: Chicoplaya, "Pavón," collected by Tafalla (lectotype, G; BM). Rio Marañón from Iquitos to the mouth of Santiago, near Pongo de Manseriche, ca. 77°30' W., *Tessmann* 4928 (type of *T. tessmannii*, photo F. M. 17942).

21. *Theobroma canumanense* Pires et Fróes, sp. nov. FIGURE 43; MAP 9

Arbor 18 m. alta pauciramosa ramulis dense ferrugineo-tomentosis, pilis crassiusculis mediocribus stellatis 8–14 radiis acutis 0.3–0.7 mm. longis instructis.

Folia rigide coriacea, petiolo crasso dense ferrugineo-tomentoso 8–10 mm. longo. Lamina oblongo-obovata vel obovato-elliptica basi paulo angustata rotundataque leviter asymmetrica apice subrotundata subite breviterque acuminata margine integra vel sursum leviter grosseque dentata, 8–20 cm. longa, 3–8.5 cm. lata, supra in sicco tabacina subnitida leviter rugosa juventute pilosa deinde glaberrima, costa nervisque secundariis filiformibus impressis ceteris paulo con-

spicuis, subtus ferrugineo-tomentosa, costa valde elevata, nervis secundariis 5 vel 6 utroque latere elevatissimis duobus basilaribus ascendentibus ceteris patulo-ascendentibus arcuatisque ad marginem decurrentibus anastomosantibus, nervis tertiariis transversis bene elevatis 3–6 mm. inter se distantibus, nervulis quaternariis elevatis transversis, minoribus prominenter minuteque reticulatis, pilis dimorphis: a) pilis stellatis albidis minutissimis dense intricatis areolas tectis, b) pilis ferrugineis crassiusculis mediocribus stellatis radiis patulis supra nervationem copiosissimis.

Flores in cymis axillaribus vel extra-axillaribus paucifloris congeste glomerati; pedunculi ad 6 mm. longi tomentosi apice 3-bracteolati, bracteolis 1–1.5 mm. longis triangularibus tomentosis; pedicelli tomentosi 1 mm. longi. Alabastra globosa crasse ferrugineo-tomentosa circa 5 mm. diam. Calyx sepalis crassiusculis carnosus in anthesin subpatulis paulo reflexis, circa 7 mm. longis, 4 mm. latis, basi 1.5 mm. longitudinaliter coalitis, intus glabris basi excepto, pilis densis crassis glandulosis ad marginem insertione praeditis extus dense stellato-tomentosis margine dense minutissime pilosulis.

Cucullus petali obovoideo-ellipsoideus circa 3–3.5 mm. longus, 2–2.2 mm. latus, carnosulus extus glaber intus 7 costis elevatis strigulosus instructus. Lamina petaloidea rubra crassa semirotundata apice emarginata, circa 2 mm. longa, 3 mm. lata, sursum utrinque minutissime pilis margine ciliata, basi subite in pediculum circa 2 mm. longum longe ciliatum contracta.

Androecium rubrum; tubus circa 1.5–1.6 mm. altus glaber. Stamina crassa curvata subspathulata sursum dilatata apice leviter emarginata, circa 6 mm. longa, 2.4–2.8 mm. lata, margine longe flexuoso-ciliata cetera glabra. Stamina filamentis glabris crassis, 1.2–1.4 mm. longis triantheriferis, lobis antherae ellipsoideis circa 0.4 mm. longis. Ovarium 1.2–1.5 mm. longum obovatum pentagonum in angulis et subapicem hirsutulum. Styli circa 2 mm. longi glabri versus apicem plus minusve liberi. Fructus ignotus.

Type in the U.S. National Herbarium, No. 2404642, collected in low, firm land, Rio Canumão, tributary of Madeira River, municipality of Borba, State of Amazonas, Brazil, October 5, 1957, by *R. L. Fróes* (No. 33783). Isotype in the herbarium of Instituto Agronomico do Norte, Belém do Pará.

Theobroma canumanense is closely related to *T. sinuosum*; its leaves and indumentum conform well with those of the type of this species showing only some differences due to the fact that the *T. sinuosum* specimens came from a young plant. The vegetative characters of the Fróes plant also coincide with the description of *T. tessmannii* given by Mildbraed, but I found a few differences which indicate that the Fróes specimens belong to a different species.

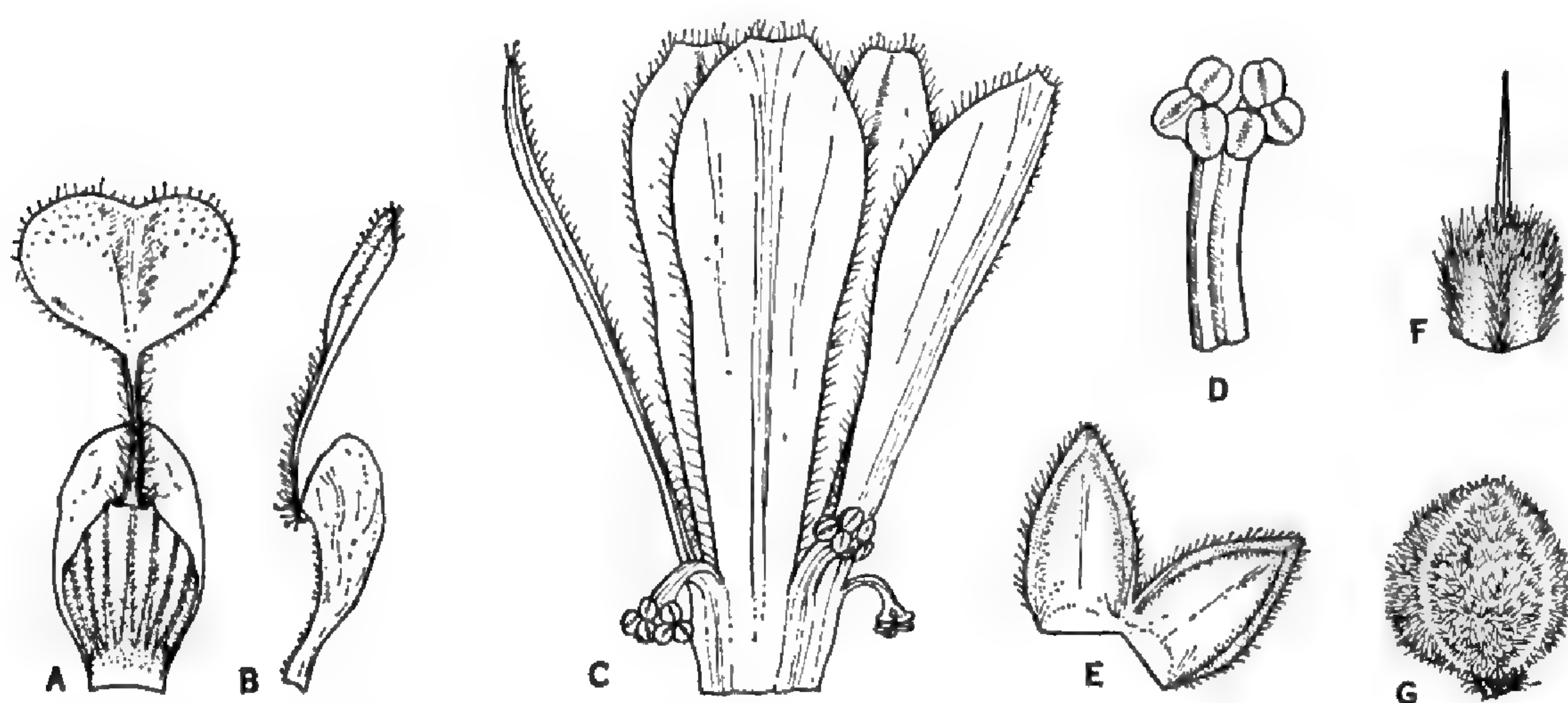


FIGURE 43.—*Theobroma canumanense* (Fróes 33783): A, petal, inside view; B, petal, lateral view, $\times 5$; C, androecium, $\times 5$; D, stamen, $\times 10$; E, sepals, inside view, $\times 2$; F, pistil, $\times 5$; G, bud, $\times 2$.

T. canumanense has smaller flowers, the sepals being only 7 mm. long; they are 10 mm. in *T. tessmannii* which also has a longer androecium (8.5 mm. high); the petals and staminodes are glabrous in the Tessmann plant according to the Mildbraed description and drawings, while they are long-ciliate in *T. canumanense*. The inflorescences are more compact in this species than in *T. tessmannii*. The photograph of the latter shows the adult leaves to be subcordate and broader at base and provided with one or two additional pairs of basal veins (not conspicuous in *T. canumanense*); the secondary nerves are more numerous (8–11 pairs) in Tessmann's plants. *T. canumanense* also differs from all related species by its extremely short pedicels (up to 1 mm. long).

COMMON NAMES.—Names and uses not recorded.

DISTRIBUTION.—Limited to the region of Rio Canumão, a tributary of the Rio Madeira in Brazil.

BRAZIL: AMAZONAS: Região do Rio Madeira, Rio Canumão, município de Borba, 5 XI 1957, R. L. Fróes 33783 (US, holotype; IAN, isotype).

Section 6. Andropetalum

Theobroma sect. *Andropetalum* Cuatr., sect. nov.

FIGURE 4

Lamina petalorum anguste spathulata longe attenuato-stipitata; cucullum 7-nervatum; staminodia crassa latissima petaloidea arcuato-reflexa petala obtegentia; stamina 3-antherifera; fructus ellipsoideo-oblongus laevis tomentosus supra basim constrictus ad apicem angustato-mammillatus epicarpio duro lignoso; semina germinatione hypogaea; folia subtus adpresse stellato-tomentosa; inflorescentiae axillares brevissimae; caulis incrementum pseudoapicale; rami

primarii ternati; calyx cymbiformis 3-lobatus, sepalis usque ad tertiam partem vel ad medium connatis.

TYPE SPECIES.—*Theobroma mammosum* Cuatr. & León.

This section comprises a single species. It is characterized by the broad, obovate-spatulate staminodes (as broad as long), which are reflexed even during anthesis, completely covering the petals, and by the reduction of the petal-laminae, which are narrower and smaller than in the closely related section *Glossopetalum*.

22. *Theobroma mammosum* Cuatr. & León

FIGURES 6, 36, 41, 42, 44; MAP 9

Theobroma mammosum Cuatr. & León, in León, Inst. Interamer. Cienc. Agr. Bol. Técn. 2:1-6, figs. 1949; León (1960) in 320, 317, fig.

TYPE.—Siquerres, Limón, Costa Rica, *León* 291.

Small tree, 6-7 m. high; trunk about 25 cm. in diameter with rather smooth, brown bark 1 mm. thick and white, hard wood; growth pseudoapical; branches ternate, from near the base, spreading or more or less descending; terminal branchlets grayish or somewhat ochraceous, appressed and minutely stellate-tomentose, later glabrous, gray, rugose; stipules subulate, acute, 4-5 (-10) mm. long, 0.6 mm. wide, deciduous.

Leaves subcoriaceous; petiole rather thick, subterete, straight or somewhat flexuous, ochraceous or ferruginous, stellate-tomentose, 5-12 mm. long; blade elliptic-oblong or oblanceolate, slightly attenuate to the apex and suddenly acuminate, slightly narrowed toward the asymmetrical base, rounded in one side, subrounded or subcuneate at the other side, the margin entire or sinuate-dentate near the apex, 10-25 cm. long, 3.5-10.5 cm. broad, including the acumen, this acute, 8-20 mm. long, glabrous above, dark green, when dry pale brownish, the costa filiform, depressed, the other nerves hardly noticeable, cinereous beneath, except for the main nerves densely and appressed stellate-tomentose, covered by thin and minute, white stellate hairs, the costa very prominent, the prominent secondary nerves 9-12 on each side, regularly parallel, subascending, curved and vanishing near the margin, the transverse tertiary nerves filiform, prominent, the lesser veins reticulate, thin, prominulous, but covered by the tomentum, the midrib, secondary, and tertiary nerves with scattered or copious, larger, thicker, spreading, stellate hairs.

Inflorescences very small, axillary, cymose with few (usually 2) flowers (1-3), the axis extremely short, tuberculate, giving rise usually to a single ferruginous-tomentose branch 8-12 mm. long, this 2- or 3-furcate at apex into 2 or 3 peduncles; peduncles very short, about 1 mm. long, 3-bracteolate at apex, each articulate to a pedicel; bracteoles linear, 2-4 mm. long, tomentose; pedicels rather thick, tomentose,

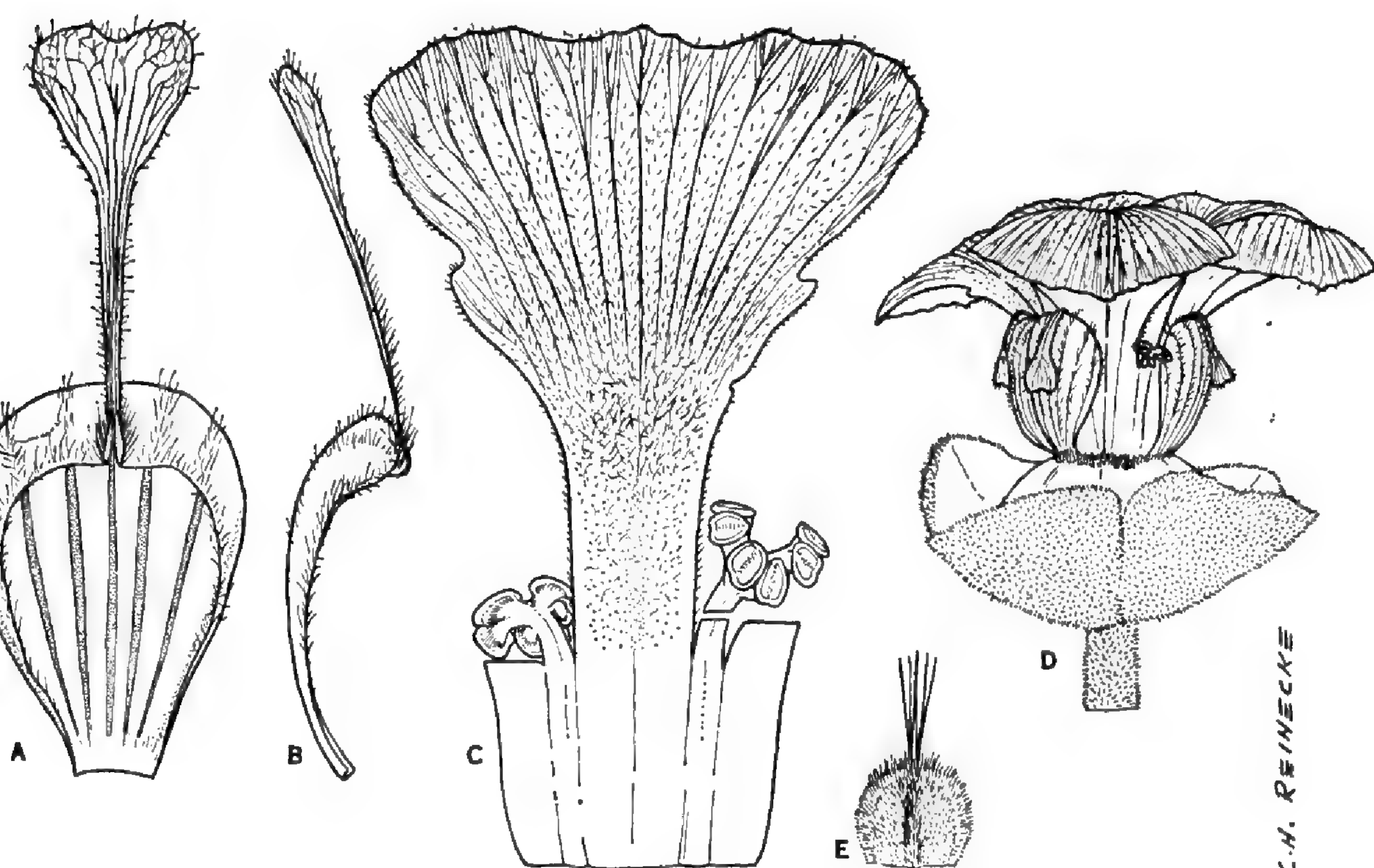


FIGURE 44.—*Theobroma mammosum* (León 1363): A, petal, inside view, $\times 5$; B, petal, laterally, $\times 5$; C, part of androecium, $\times 5$; D, flower in anthesis, $\times 2.5$; E, gynoecium, $\times 5$.

8–12 mm. long; buds globose, densely ferruginous tomentose, about 1 cm. in diameter.

Sepals 11–12 mm. long, 5–6 mm. broad, thick, triangular-ovate, united completely by pairs or by 2 and 3, and all five in the lower third, forming a cupular, umbilicate, 2 or 3 short-lobate calyx, yellowish green inside, red tinged, glabrous except for the glandular, thick, erect, fasciculate, congested trichomes at the inner base, these 0.4–0.7 mm. long, densely, thickly, stellate-tomentose outside, greenish ochraceous or ferruginous.

Petal-hoods about 7–8 mm. long, 5–7 mm. broad, elliptic-obovate, broadly rounded-cucullate at apex, dark red, rather carnose with 7 thick nerves, between the nerves veined with yellowish or rose by transmitted light, minutely papillose inside, rugulose outside with sparse, long, acute, straight or slightly flexuous hairs throughout, these more copious at margin; petal-lamina erect in full anthesis, narrow, thick, dark red or purplish red, truncate-spatulate or slightly emarginate, usually plicate, with long, ferruginous, slightly flexuous hairs, these scattered outside, abundant at margin and inside, 3 mm. long, 2.5–3 mm. broad, gradually narrowed toward the base into a plicate pedicel about 4 mm. long, 0.5 mm. wide.

Androecium purplish red or dark red, the tube carnose, about 4 mm. high, 3–4 mm. broad, glabrous; staminodes large, petaloid, reflexed, the lower part thick, carnose, toward the apex gradually thinner, membranaceous, transparent-veined, obovate-spatulate, subtruncate and slightly sinuate at apex, laterally usually 1-dentate, the lower half suddenly narrower, about 11–12 mm. long, 10–12 mm. broad at top and 2.5 mm. wide at base, glabrous or with sparse hairs near the top outside, with copious, ferruginous, simple or stellate, rather long hairs inside; filaments thick, glabrous, about 1 mm. long, shortly 3-furcate, 3-antheriferous, the lower branchlet extremely short, the other two lateral about 1 mm. long; anther lobes ellipsoid, suborbicular, about 1 mm. long after anthesis; ovary subglobose, slightly 5-angulate, whitish, densely tomentose-hirsute, about 1.8 mm. high and thick; styles 2 mm. long, glabrous, erect, acute, connivent, only united at base.

Fruit at maturity 16–22 cm. long, 6–8.5 cm. broad, cylindric-oblong, terete or seldom slightly pentagonous, broad and umbilicate at base, strongly contracted and slightly pentagonal above the base, suddenly narrowed near the apex forming a mammiform, umbilicate end 2–3 cm. long and 2–2.5 cm. broad. Pericarp coriaceous, hard, smooth or slightly verrucose downward, pale green, covered by dense, short, ferruginous tomentum, the woody epicarp 1.5–2 mm. thick with a tomentose epiderm outside, the mesoendocarp carnose, white, about 7 mm. thick; pulp enveloping each seed fleshy, fibrous, white; seeds ovoid-amygdaloid, brownish, 22–27 mm. long, 14–17 mm. broad, 10–13 mm. thick; cotyledons white; germination hypogeous.

COMMON NAME.—Cacao silvestre.

DISTRIBUTION.—Eastern coastal mountains of Costa Rica, where it is extremely rare in primary forest. It has been found wild only twice, at altitudes from 300 to 800 meters. Cultivated in few agricultural experimental stations.

COSTA RICA: LIMÓN: La Lola, 100 m. alt., 12 V 1948, *Escamilla*, s.n. (MO). Siquirres, Finca La Lola, 300 m. alt., I 1949, *León* 291 (holotype, TURRI). La Lola, cerca de Madre de Dios, 100 m. alt., cultivated, 30 I 1949, *León* 1363 (paratype, F, TURRI). Ibidem, Experimental Station I.I.C.A., cultivated; tree 6 m., stem 20–25 cm. diam., leaves chartaceous, firm, green above, pale beneath, branches ternate, growth pseudoapical, flowers dark red and brown red, fruit ellipsoid, contracted at apex, 6 XI 1961, *Cuatrecasas & Paredes* 26535 (US).

HEREDIA: Puerto Viejo, Sarapiquí, 700–800 m. alt., IV 1959, *Holdridge* 146 (TURRI).

CARTAGO: Turrialba, grounds of I.I.C.A., cultivated, 600 m. alt., 4 XI 1961, *Cuatrecasas & León* 26516 (US).

TRINIDAD: River State Diego Martinez, I.C.T.A., Field 19, cultivated from seed received from Belém do Pará; tree 8 m. high, stem rugose-tuberculate, brown, abundant dry fruits hanging from branchlets, 1 IX 1961, *Cuatrecasas & Cope* 25791 (US).

Hybrids

Theobroma angustifolium Moc. & Sessé ♂ × **mammosum** Cuatr. & León ♀.

Trinidad, I.C.T.A., *Cuatrecasas & Cope* 25800. Well-developed tree, with intermediate characters.

Theobroma grandiflorum (Spreng.) Schum. × **obovatum** Klotzsch.

Belém do Pará, Brazil, Museu Goeldi, arvore 480, 22 XII 1958, *Cavalcante* 937 (MG, US).

Theobroma grandiflorum (Spreng.) Schum. ♀ × **subincanum** Mart. ♂.

Hybrid fertile obtained by Addison and Miranda (1951) 13. Intermediate features of parents.

Theobroma grandiflorum (Spreng.) Schum. ♀ × **obovatum** Kl. ♂.

Brazil. Fertile hybrid obtained by Addison (1951) 10, *pl. 1, fig. 3, pl. 2, fig. C*. F. cultivated at Belém do Pará, 6 XI 52, *Pires* 4343 (IAN). Ibidem, *Pires* 4344 (IAN).

Theobroma mammosum Cuatr. & León ♂ × **simiarum** Donn. Smith. ♀

Costa Rica, Turrialba IICA, robust young trees obtained by Soria.

Theobroma mammosum Cuatr. & León ♀ × **simiarum** Donn. Smith ♂.

Costa Rica, Turrialba, IICA, robust young trees obtained by Soria.

Theobroma obovatum Klotzsch ♂ × **subincanum** Mart. ♀.

Fertile hybrid obtained by Addison and Miranda (1951) 14, *pl. 13, fig. 13, pl. 4, fig. C*. Also found spontaneous by Cope & Holliday in Colombia: Río Caquetá, Remolino, tree 11-12m., with some characters of *T. obovatum* and others of *T. subincanum*, 2 V 1953; it has almost smooth pods but bears flobose, woolly pubescence on the young shoots and leaves, *Holliday & Cope* T 122 (COL, TRIN, US). Caquetá, Río Caguán, tree 8 m., 27 IV 1953, *Cope & Holliday* T 117 (COL, TRIN). Brazil, Amazonas, Fonte Boa; tree 15 m. alt. "cupurana," *Fróes* 20648 (IAN, US). Trinidad, ICTA, experimental camps, *Cuatrecasas & Cope* 25797 (US).

Theobroma speciosum Willd. ex Spreng. ♂ × **sylvestre** Mart. ♀.

Belém do Pará, Brazil, 6 XI 1952, *Pires* 4345 (IAN, COL). Experimental hybrid by Addison. It has intermediate characters as described and illustrated by Addison & Miranda (1951) 14, *pl. 5 fig. 3, pl. 6, fig. C*.

Theobroma speciosum Willd. ex Spreng. ♀ × **sylvestre** Mart. ♂.

Belém do Pará, Brazil. Experimental hybrid obtained by Addison, similar to the former. Addison & Miranda (1951) 15.

At the Instituto Interamericano, Costa Rica, Dr. Soria (1961) tried to hybridize *T. cacao* with *T. angustifolium*, *mammosum*, *simiarum*, and *bicolor*. The cross *T. angustifolium* ♂ × *cacao* ♀ gave small

plants which did not grow more than about 10 cm. in two years. *Theobroma cacao* ♀ × *mammosum* ♂ gave fruits, but the seeds were very weak; the same happened with *T. cacao* ♀ × *simiarum* ♂. The cross *T. bicolor* ♂ × *cacao* ♀ was negative. See also Addison and Miranda in the Historical Sketch above.

Rejected Names and Excluded Species

Theobroma Kalagua de Wildeman, Bull. Herb. Boiss. 7:957, pl. 11. 1899.

TYPE.—Panama, *Patin*, s.n. (lectotype, BR, leaf) (F. M. Photo 40742).

This species was described by de Wildeman as very remarkable, because of the extraordinary combination of flowers similar to those of *T. angustifolium* and *T. simiarum*, fruits resembling *T. simiarum*, and quite different leaves which although resembling those of *T. angustifolium* in shape differed by the lack of pubescence. But Patin gave assurance to Wildeman that these different parts came from a single tree. De Wildeman wrote: “qui appartiendraient sans le moindre doute à la même plante. Une confusion aurait cependant pu être possible parce que le *Th. simiarum* existe également en Colombie, où M. Ch. Patin, qui s'adonne à la recherche des plantes utiles, l'a découvert à Choco, province de Cauca” (Wild. p. 958). In the U.S. National Herbarium, attached to a herbarium sheet (1,382,338), is a letter sent to J. Donnell Smith by Ch. Patin, dated Brussels 19 Oct. 1900. Here Patin states “As concerns *T. Kalagua* . . . there was a doubt about the leaves used to determine the specy [sic]: the young plants which we have just got here from seeds have proved that it occurred really a mistake in the description made of the leaves brought to me by my collector.” This contradicts the earlier assurances given by Patin about all his specimens having been collected from a single tree and shows that he was not the collector himself. Later on Patin writes, “I think that the *T. Kalagua* is just your *T. Simiarum*.” Patin never explained where his specimens were collected. Probably they came from the region of Panamá. Regarding the specimens sent with the above cited letter, the seedling leaves and small fragments of fruits might well be those of *T. simiarum*.

To clear up this question, in 1953 I asked Dr. Robyns, director of the Jardin Botanique de l'Etat, Brussels, to send me the material of *T. kalagua* preserved at that herbarium. Very kindly, Dr. Robyns sent me the only existing herbarium sheet of the type material of *T. kalagua*, which is represented only by one leaf, undoubtedly the same used to illustrate the plate in the publication. To a further request to Dr. Robyns the answer was given that no other material

of this species existed except for some fruits which "selon toute vraisemblance appartiennent au matériel *Patin* s.n. recolté en 1899, se trouvaient dans nos collections de fruits."

Examination of the *Patin* specimens proves that the leaf mounted on this sheet at BR (photo F. M. No. 40742) is the original *Patin* leaf used for de Wildeman's illustration and that this leaf belongs to *Theobroma cacao*. This leaf is the only unquestionable part of the type apparently existing, and I select it as the lectotype. The three fruits received on loan from Brussels labeled *T. kalagua* were: 1) A half shell, to be discarded as belonging to *Theobroma bicolor*. 2) An entire pod with a modern label from "J. Bot. Br." reading "*Th. Kalagua* Wild. Colombie, sans date Coll. Patin." This fruit is smooth, ellipsoid, oblong, slightly attenuate and rounded at apex and broadly rounded, umbilicate at base, 18–20 cm. long, and 8.8 cm. broad; the surface is tomentose, the woody epicarp about 1.5 mm. thick, the dried, spongy mesoendocarp 2–4 mm. thick; a fragment of this shell is lacking, and this could be the fragment of fruit sent by Patin to Donnell Smith and preserved at the U.S. National Herbarium (1,382,338). This fruit is not that used for the illustration, because the original was sectioned; furthermore, this pod looks somewhat more oblong than the one figured in the plate. It may well belong to *T. simiarum*, as may also the seedling leaf sent to Donnell Smith. 3) The third fruit received from Brussels bears two labels; one reads "*Theobroma kalagua*, Colombie, Chocó, Prov. de Cauca, leg. Ch. Patin 1899," and the number 823; the other label reads "*Theobroma simiarum* D. Sm. Colombie, leg. Ch. Patin"; it consists of half a shell whose section is ovate-ellipsoid, 19 cm. long and 14.2 cm. broad and about 2 cm. thick; the woody epicarp is 1.5–2 mm. thick; the thick mesoendocarp is compact. It is different from all species of *Theobroma* known to date; it might be an undescribed species, but it could also belong to another genus.

In conclusion, we may infer that Patin gathered several specimens of different *Theobroma* species collected by different persons and coming from several places (Panama, Chocó . . .). The flowers described by de Wildeman could well be flowers of *T. angustifolium* or *T. simiarum*; the possibility of their growing in Panama, perhaps planted, cannot be discarded. They also could have been flowers from trees of *T. stipulatum*, *T. chocoense*, or from some undescribed species. An important character of the flower, its color, was not mentioned by Patin. The fruit shown in the plate is thicker than that of *T. simiarum*; it recalls very much that of *T. grandiflorum*, a species more or less widespread in gardens, and it is also similar to that of *T. chocoense* and *T. stipulatum*. It may also belong to an undescribed species. To ascertain to what species such a fruit belongs,

it would be necessary to see at least two associated organs from the same tree, that is to say fruit and leaves, fruit and flowers, or, also, flowers and leaves. The above comments on the available data prove the disorderly way of Patin's work and his unreliability. There is no reason to believe that the flowers and fruits of Patin's collections were brought from the same tree or from the same species. Patin never mentioned the locality of the specimens sent to de Wilde-man or who collected them. Colombia is always cited but at that time Panama was part of Colombia. At present the only identifiable Patin specimen from his syntypes is the leaf (BR) and that is *T. cacao*. Consequently, *T. kalagua* becomes a synonym of *T. cacao*.

Theobroma guianense (Aubl.) Gmel., Syst. Veg. ed 13, 2:1151. 1796.

Cacao guianensis Aubl. Pl. Guian. 2: 683, pl. 275. 1775.

SYNTYPES.—Aublet illustrations (l.c.) and specimens at British Museum (Natural History).

Under *Cacao guianensis*, Aublet gave a detailed and illustrated description made up of a mixture of three different species. There is complete agreement between the description of each part and the corresponding illustration. The flowers were described from specimens of *Theobroma cacao* L.; the branches and leaves from *T. subincanum* Martius; the fruits cannot be identified with any other species included in Bernoulli's and Schumann's treatments. The illustration of this fruit (*Pl. 275, figs. 16 & 17*) agrees unmistakably with only one recent collection of *Theobroma* fruits, namely that from French Guiana by Benoist, which is the type of *T. velutinum* Benoist. Aublet's short diagnoses of the fruit, especially the French description "l'ovaire devient une capsule ovoïde à cinq arrêtes arrondies saillantes" also agree perfectly with it. It seems that Aublet considered the most typical part of his "species" the fruit, since he headed the description of his *Cacao guianensis* with a short definition based only on the fruit: "CACAO (*Guianensis*) fructu ovato, quinquangulati, tomentoso, rufescente (Tabula 275)" (p. 683); furthermore, as Sandwith pointed out, the French name given by Aublet [*Le Cacaoier anguleux*. (*Planche 275*)] was taken from the same diagnosis. Thanks to Benoist we know now that this kind of fruit belongs to a species with a kind of leaves very different from those described by Aublet, the species described by Benoist as *T. velutinum*.

But the nomenclatural problems have to be solved on the basis of types according to the International Code. At the British Museum there are preserved Aublet specimens and among them type specimens of *Cacao guianensis* which are syntypes. In 1954, I could identify by close examination an herbarium sheet (with foliage, one flower,

and an immature fruit) as belonging to *T. subincanum* Mart.; this specimen agrees with the description and drawings given by Aublet for the leaves and branchlets; this evidence could easily incline us to use this specimen as lectotype for *C. guianensis*. But in the carpological collection of the British Museum there is a fragmentary fruit, also a syntype of Aublet's species, which belongs to *T. cacao*.

Until now, there has been only confusion about the identity of *Theobroma guianense*. Bernoulli (p. 7) wrote: "*Cacao guianensis* bleibt somit eine vollstaendig ungewisse Art. Sie scheint auch von keinem weitem Autor gesehen worden zu sein, sondern immer nach Aublet citiert zu werden." Schumann placed it as synonym of *Theobroma cacao*, surely on account of its flowers. Chevalier considered the species synonymous with *T. speciosum* Willd., erroneously interpreting Aublet's descriptions and drawings of the leaves and a photograph of the Aublet herbarium specimen (syntype) at the British Museum; these, as I have pointed out above, belong to *T. subincanum* Mart. He also identified the Benoist collections of *T. velutinum* erroneously as *T. speciosum*.

Consequently, *Cacao guianensis* Aubl. is not a true species, but a mixture of three species. Therefore the Aublet "species" and name has to be rejected as "nomen confusum" (articles 63(3), 65, and 66 of the Code of Nomenclature). The name *Theobroma guianense* has never been consistently used in monographs and general books for any known species.

"**Theobroma fossilium**" Berry, Proc. U.S. Nat. Mus. 75(24):8, pl. 1, figs. 13, 14. 1929.

In regard to this unfortunate name, the following opinion of R. W. Brown, former paleobotanist of the U.S. Geological Survey, is final: "This specimen, considered by Berry to be the first fossil record of *Theobroma*, is a section of the forepart of a reptilian jaw. Berry mistook the bony structure for the pulp, and the teeth for the seeds of a chocolate-bean pod. Although described among Tertiary plants, the specimen, as stated by Berry, came from near Leiva, Department of Boyacá, Colombia, where Cretaceous strata crop out." (Journ. Washington Acad. Sci. 36:353. 1946).

Theobroma alba Bernoulli, Uebers. Art. Theobroma 14. 1869; Jumelle (1899) 35; De Wildeman (1902) 98. 1902.

TYPE.—Essequibo et Cuyaunic, British Guiana, *C. F. Appun* 1, 1860 (holotype, Herbarium Hookerianum, K).

The type of this species consists of leaves of a young, sterile plant of the genus *Licania*. I have identified it by comparison from the abundant material existing in the Royal Botanic Gardens, Kew, with

L. venosa Rusby, a widespread species of the Guianas. The following new combination is necessary:

- Licania alba** (Bernoulli) Cuatr., comb. nov. *Theobroma alba* Bernoulli, Uebers. Art. *Theobroma* 14. 1869. *Licania venosa* Rusby, Descr. New Sp. So. Am. Pl. 26. 1920.
- Theobroma albiflorum** (Goudot) De Wildeman, Pl. Trop. Gr. Cult. 90. 1902 = *Herrania albiflora* Goudot, Ann. Sci. Nat. III, 2:230, pl. 5. 1844.
- Theobroma aspera** (Karsten et Triana ex Triana) Van Hall, Cacao, ed. 2, p. 49. 1932. (*Brotobroma aspera* Karsten et Triana ex Triana, Nuev. jen. y esp. fl. Neo-Granat. 12. 1854) = *Herrania nitida* (Poepp.) Schultes, Caldasia 2:16, 17, pl. 1943.
- Theobroma augusta** L. Syst. Nat. 3:233. 1776; Willd. Sp. Pl. 3:1424. 1803 = *Abroma augusta* (L.) L. f. Suppl. 341. 1781.
- Theobroma balaënsis** (Preuss) De Wildeman, Pl. Trop. Gr. Cult. 89. 1902 = *Herrania balaensis* Preuss, Exped. Centr. und Süd-Amerika 253, pl. 7. 1901.
- Theobroma camargoanum** (Schultes) Ducke, Bol. Técn. Inst. Agron. Norte 28:15. 1954 = *Herrania camargoana* Schultes, Bot. Mus. Leaf. Harvard Univ. 14:120, pl. 29, 32. 1950.
- Theobroma celtifolia** Salisburg, Prodr. 387. 1796 = *Guazuma ulmifolia* Lam. Encycl. Méth. 3:52. 1789.
- Theobroma guazuma** L. Sp. Pl. 782. 1753 = *Guazuma tomentosa* H. B. K. Nov. Gen. Sp. 5:320. 1823. Freytag (1951) 214.
- Theobroma hastata** Chevalier, Rev. Bot. Appl. 26:273. 1946, *nomen nudum*; *lapsus calami* for *T. sagittata* Pavón ex Chevalier.
- Theobroma laciniifolium** (Goudot ex Triana et Planchon) De Wildeman, Pl. Trop. Gr. Cult. 90. 1902 = *Herrania laciniifolia* Goudot ex Triana et Planchon, Prodr. Fl. N. Granat. 209. 1862.
- Theobroma mariae** (Martius) Schumann in Mart. Fl. Bras. 12³:71, pl. 15. 1886 = *Herrania mariae* (Mart.) Decaisne ex Goudot Ann. Sci. Nat. III, 2:233. 1844.
- Theobroma montana** Goudot ex Bernoulli, Uebers. Art. *Theobroma* 15. 1869, *nomen nudum*. No description.
- Theobroma nitidum** (Poepp. et Endl.) Schumann in Mart. Fl. Bras. 12³:72. 1886. (*Abroma nitida* Poepp. et Endl., Nov. Gen. Sp. Pl. 3:73. 1845) = *Herrania nitida* (Poepp. et Endl.) Schultes, Caldasia 2:16, 17, pl. 1943.
- Theobroma purpureum** Pittier, Repert. Sp. Nov. Fedde 13:319. 1914 = *Herrania purpurea* (Pittier) Schultes, Caldasia 2:333. 1944.
- Theobroma pulcherrimum** (Goudot) De Wildeman, Pl. Trop. Gr. Cult. 89. 1902 = *Herrania pulcherrima* Goudot, Ann. Sci. Nat. III, 2:232, pl. 5. 1844.
- Theobroma sagittata** Pavón ex Chevalier, Rev. Bot. Appliq. 26:274. 1946, *nomen nudum* = *Herrania nitida* (Poepp. et Endl.) Schultes, Caldasia 2:16, 17, pl. 1943.
- Theobroma tomentosa** (H. B. K.) Gómez, An. Hist. Nat. 19:217. 1890 = *Guazuma tomentosa* H. B. K. Nov. Gen. Sp. 5:320. 1823.
- Theobroma undulata** Pavón ex Chevalier, Rev. Bot. Appliq. 26:268. 1946, *nomen nudum*: *lapsus calami* for *T. sinuosum* Pavón ex Huber.

Collections Cited

- | | |
|--|--|
| <p>ACOSTA SOLÍS, M., & GILER, M.
 12392 gileri
 12423 gileri
 ALLEN, P. H.
 3105 grandiflorum
 4593 bicolor
 6259 angustifolium
 6341 angustifolium
 APPUN, C. F.
 1 Alba
 ARAQUE, J., & BARKLEY, F. A.
 18C745 hylaeum
 ARCHER, W. A.
 7517 subincanum
 7537 obovatum
 7549 grandiflorum
 7551 microcarpum
 7619 speciosum
 7721 speciosum
 7734 grandiflorum
 7820 subincanum
 ASPLUND, E.
 10271 bicolor
 12911 subincanum
 13410 subincanum
 AUBLET, J. B. C. F.
 s.n. cacao (fruit)
 s.n. subincanum
 BAFOG (BUREAU AGR. ET FORESTIER
 GUYANAIS)
 136M velutinum
 7386 velutinum
 BAILEY L. H.
 s.n. angustifolium
 BAKER, C. F.
 62 grandiflorum
 421 grandiflorum
 2102 angustifolium
 BAKER, R. E. D.
 16 grandiflorum
 33 subincanum
 34 bicolor
 37 glaucum
 38 subincanum
 s.n. angustifolium</p> | <p>BAKER, R. E. D., BARTLEY, B. G., &
 HOLLIDAY, P. C.
 31 subincanum
 32a subincanum
 BAKER, R. E. D., & COPE, F. W.
 2 bicolor
 3 subincanum
 4 subincanum
 5 grandiflorum
 6 grandiflorum
 7 subincanum
 11 glaucum
 11a bicolor
 12 subincanum
 13 subincanum
 21 subincanum
 25 subincanum
 26 bicolor
 27 obovatum
 28 microcarpum
 29 microcarpum
 30 obovatum
 31 subincanum
 32 subincanum
 BARTLEY, B. G., & HOLLIDAY, P. C.
 T 46 grandiflorum
 T 47 bicolor
 T 65 subincanum
 T 66 bicolor
 T 68 subincanum
 T 69 glaucum
 T 70 glaucum
 T 71 subincanum
 T 72 subincanum
 T 74 glaucum
 T 75 subincanum
 T 166 hylaeum
 BENOIST, R.
 516 velutinum
 BERNOULLI, G.
 94 bicolor
 95 angustifolium
 BERNOULLI, G., & CARIO, R.
 3188 angustifolium
 3145 bicolor</p> |
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- BLACK, G. A.
 47-1496 obovatum
 47-1502 grandiflorum
 47-1889 speciosum
 BLACK, G. A., CORDEIRO, E. & FRANCISCO, J.
 52-14649 microcarpum
 52-14655 speciosum
 BLACK, G. A. & LEDOUX, P.
 50-10644 sylvestre
 BLACK, G. A. & SCHULTES, R. E.
 46-61 grandiflorum
 46-61 (USDA) subincanum
 46-III grandiflorum
 BOEHLMER, F. DE
 12229 bicolor
 BONPLAND, A.
 s.n. bicolor
 BRENES, A. M.
 12333 bicolor
 BRITISH HONDURAS FORESTS CON-
 SERVATION
 H2192/29 bicolor
 BROADWAY, W. E.
 8935 angustifolium
 BURCHELL, W. J.
 9375 grandiflorum
 9467 grandiflorum
 B. W. [BOSCHWEZEN]
 1161 velvutinum
 CALDERÓN, S.
 627 bicolor
 630 angustifolium
 23610 bicolor
 CAMARGO, F. C.
 8 microcarpum
 2395 speciosum
 CAPUCHO, P.
 397 speciosum
 CARDEÑOSA, B., MURGUEITIO,
 P. R. & BARKLEY, F. A.
 17C934 bicolor
 CARDONA, F.
 2379 subincanum
 CAVALCANTE, P.
 310 bicolor
 339 obovatum
 937 grandiflorum × obo-
 vatum
 938 subincanum
- COPE, F. W., & HOLLIDAY, P. C.
 (see Holliday & Cope)
 COOK, O. F.
 4 bicolor
 COOK, O. F., & DOYLE, C. B.
 50 bicolor
 COOK, O. F., & GRIGGS, R. F.
 756 bicolor
 COOPER, J. J.
 10244 simiarum
 COOPER, G. P., & SLATER, G. M.
 242 angustifolium
 COWAN, R. S.
 38164 subincanum
 38186 subincanum
 CUATRECASAS, J.
 6890 subincanum
 7277 subincanum
 7178A subincanum
 14897 cirmolinae
 15336 cirmolinae
 15700 cirmolinae
 16160 bernouillii subsp. capil-
 liferum
 16526A bicolor
 16544 nemorale
 16896 chocoense
 17034 bernouillii subsp. capil-
 liferum
 17034A bernouillii subsp. capil-
 liferum
 17350 bernouillii subsp. capil-
 liferum
 17350A bernouillii subsp. capil-
 liferum
 17503 nemorale
 17738 nemorale
 21291 nemorale
 21339 stipulatum
 CUATRECASAS, J., & COPE, F. W.
 25788 obovatum
 25789 angustifolium
 25790 angustifolium
 25791 mammosum
 25792 simiarum
 25794 simiarum
 25795 bicolor
 25797 obovatum × subincanum
 25800 angustifolium × mammo-
 sum
 25801 grandiflorum

CUATRECASAS, J., COPE, F. W., &
BARTLEY, B. G.

- 25780T grandiflorum
25781T grandiflorum
25782T nemorale
25783T obovatum
25784T bicolor
25785T subincanum
25786T bicolor
25787T bicolor

CUATRECASAS, J., & LEÓN, J.

- 26515 simiarum
26515A simiarum
26516 mammosum

CUATRECASAS, J., & PAREDES, A.

- 26534 bicolor
26535 mammosum
26536 simiarum
26537 angustifolium
26538 microcarpum

CUATRECASAS, J., & WILLARD, L.

- 26007 nemorale
26051 nemorale
26074 chocoense
26167 gileri

CUFODONTIS, G.

- 92 bicolor
599 simiarum

DAHLGREN, B. E., & SELLA, E.

- 10 microcarpum
438 grandiflorum
634 grandiflorum
733 grandiflorum
739 grandiflorum

DAVIDSON, G. W. R.

- s.n. bicolor

DAWE, M. T.

- 83 bicolor

DODGE, C. W., & GOERGER, V. F.

- 9420 simiarum

DODGE, C. W., & NEVERMANN

- 7164 simiarum

DODGE, C. W., & THOMAS, W. S.

- 6399 angustifolium

DUCKE, A.

- 100 sylvestre
103 sylvestre
265 obovatum
281 speciosum
283 microcarpum
598 grandiflorum
4878 sylvestre
6773 microcarpum

- 6823 obovatum

- 7200 subincanum

- 7202 bicolor

- 7202B bicolor

- 7216 sylvestre

- 7397 bicolor

- 7638 bicolor

- 7679 subincanum

- 7704 obovatum

- 7822 sylvestre

- 7884 speciosum

- 7975 speciosum

- 10669 sylvestre

- 12187 sylvestre

- 14734 sylvestre

- 14925 subincanum

- 16458 grandiflorum

- 16464 subincanum

- 16466 microcarpum

- 21044 obovatum

- 21045 microcarpum

DUQUE JARAMILLO, J.

- 1205 bicolor

- 4403A bicolor

EGGERS, H. F. A.

- 14244 bicolor

ELLENBERG, H.

- 2551 obovatum

- 2565 speciosum

ESCAMILLA, G.

- s.n. mammosum

FAGERLIND, F., & WIBOM, G.

- 2371 bicolor

FERNÁNDEZ P, A.

- 2275 subincanum

FOSBERG, F. R.

- 21310 bicolor

FRANCISCO, J.

- 1966 grandiflorum

FRÓES, R. L.

- 20463 sylvestre

- 20518 subincanum

- 20555 subincanum

- 20556 sylvestre

- 20625 bicolor

- 20645 glaucum

- 20646 obovatum

- 20648 obovatum × subin-
canum

- 20655 sylvestre

- 20750 microcarpum

- 20885 glaucum

- 20942 glaucum

- | | | |
|--------------------------------------|--------------|-----------------------------------|
| 21162 | subincanum | GOELDI, ANDREAS |
| 21482 | subincanum | 4225 subincanum |
| 21556 | grandiflorum | 4226 obovatum |
| 23343 | subincanum | 4228 microcarpum |
| 23926 | obovatum | GONGGRYP, J. W. |
| 23963 | microcarpum | 4108 velutinum |
| 25554 | sylvestre | 4127 velutinum |
| 26526 | speciosum | 4148 velutinum |
| 28382 | sylvestre | GOUDOT |
| 29732 | speciosum | s.n. bicolor |
| 30180 | speciosum | GUERRERO, H. |
| 30432 | speciosum | 26074 chocoense |
| 31414 | speciosum | HANBURY |
| 33783 | canumanense | 9471 grandiflorum |
| 33788 | sylvestre | HART, J. H. |
| 34663 | subincanum | 158 bicolor |
| 34949 | sylvestre | 5381 augustifolium |
| FRÓES, R. L., & FILHO, J. P. | | HOFFMANNSEGG, W. |
| 29465 | sylvestre | s.n. speciosum |
| GARCÍA BARRIGA, H. | | HOLDRIDGE, L. R. |
| 11178 | bicolor | 146 mammosum |
| 14203 | subincanum | 5133 gileri |
| 14224 | subincanum | s.n. bicolor |
| 14253 | subincanum | HOLLIDAY, P. C. |
| 14380 | glaucum | T 43 subincanum |
| 14416 | bicolor | T 139 cirmolinae |
| 15139 | subincanum | T 140 cirmolinae |
| GARCÍA BARRIGA, H., SCHULTES, R. E., | | T 141 nemorale |
| & BLOHM, H. | | T 142 bernouillii subsp. capil- |
| 16064 | subincanum | liferum |
| GARDNER, C. A. | | T 143 chocoense |
| 870 | bicolor | T 144 chocoense |
| GENTLE, P. H. | | T 145 bernouillii subsp. capil- |
| 3464 | bicolor | liferum |
| GEOFFROY, | | T 146 nemorale |
| s.n. speciosum | | T 147 nemorale |
| GILER, M. | | T 148 nemorale |
| 162 | gileri | T 149 nemorale |
| 168 | gileri | HOLLIDAY, P. C., & BARTLEY, B. G. |
| GILER, M., & PATIÑO, V. M. | | T 163 gileri |
| 164 | gileri | T 165 stipulatum |
| 165 | gileri | T 167 gileri |
| 166 | gileri | T 172 bernouillii subsp. capil- |
| GINZBERGER, A. | | liferum |
| 802 | speciosum | T 173 nemorale |
| GINZBERGER, A., & HAGMANN, M. | | T 175 stipulatum |
| 801 | subincanum | T 176 chocoense var. bullatum |
| GINZBERGER, A., & ZERNER, H. | | T 177 bernouillii subsp. capil- |
| 800 | grandiflorum | liferum |
| GLAZIOU, A. F. M. | | T 178 bernouillii subsp. capil- |
| 9633 | speciosum | liferum |
| 9633a | subincanum | |
| 9643 | grandiflorum | |

- HOLLIDAY, P. C., & COPE, F. W.
 T 77 bicolor
 T 79 glaucum
 T 79A glaucum
 T 81 subincanum
 T 90 obovatum
 T 91 subincanum
 T 94 glaucum
 T 95 obovatum
 T 96 glaucum
 T 98 obovatum
 T 101 subincanum
 T 103 subincanum
 T 114 obovatum
 T 115 glaucum
 T 116 subincanum
 T 117 obovatum × subincanum
 T 118 glaucum
 T 119 obovatum
 T 122 obovatum × subincanum
 T 123 obovatum
 T 124 subincanum
 T 125 microcarpum
 HUBER, H.
 162 subincanum
 1567 speciosum
 1748 speciosum
 4008 grandiflorum
 4295 obovatum
 7081 microcarpum
 HUMBOLDT, A., & BONPLAND, A.
 s.n. bicolor
 IDROBO, J. M., & SCHULTES, R. E.
 776 subincanum
 INPA (INSTITUTO NACIONAL DE
 PESQUISAS DA AMAZONICA, MANAOS)
 1966 grandiflorum
 2125 sylvestre
 JOBERT, DR.
 903 speciosum
 JOHNSON, H.
 237 bicolor
 KARSTEN, G.
 s.n. glaucum
 KILLIP, E. P., & SMITH, A. C.
 30006 bicolor
 30011 grandiflorum
 30320 grandiflorum
 KLUG, G.
 87 subincanum
 857 subincanum
 1523 bicolor
 2021 bicolor
 2983 obovatum
 KRUKOFF, B.
 1080 speciosum
 1117 speciosum
 1274 grandiflorum
 1644 microcarpum
 1668 obovatum
 5295 speciosum
 5388 obovatum
 5759 obovatum
 6203 microcarpum
 6263 obovatum
 6592 microcarpum
 7016 subincanum
 8226 subincanum
 8275 obovatum
 8280 microcarpum
 9019 bicolor
 KUHLMANN, J. G.
 18110 subincanum
 LABROY
 s.n. grandiflorum
 LANGE
 12056 bicolor
 LEHMANN, F. C.
 7909 bicolor
 9021 bicolor
 LEÓN, J.
 291 mammosum
 937 angustifolium
 1363 mammosum
 3189 simiarum
 4267 angustifolium
 4832 gileri
 LINDEMAN, J. C.
 5725 simiarum
 LITTLE, E. L., & LITTLE, R. R.
 9544 subincanum
 9598 bicolor
 LLANO, E.
 s.n. bicolor
 LÓPEZ, J. R.
 s.n. angustifolium
 LUCAS, A.
 1 bernouillii subsp. asclepi-
 adiflorum
 LUETZELBURG, PH. V.
 22007 grandiflorum
 22079 subincanum
 23065 bicolor
 23287 grandiflorum
 23895 bicolor

- MARTIUS, C. E. P.
 862 bicolor
 863 bicolor
 864 bicolor
 865 bicolor
 871 sylvestre
 872 subincanum
 873 p.p. grandiflorum
 873 p.p. subincanum
 874 grandiflorum
 875 grandiflorum
 876 grandiflorum
 884 microcarpum
 885 microcarpum
 886 microcarpum
 887 sylvestre
 888 sylvestre
 889 sylvestre
 890 sylvestre
 891 sylvestre
 893 subincanum
 894 subincanum
 895 subincanum
 896 subincanum
 897 subincanum
 898 subincanum
 899 subincanum
 900 subincanum
 Observ. 2832 sylvestre
 Observ. 2890 microcarpum
- MATUDA, E.
 16690 bicolor
 16733 bicolor
 16840 bicolor
- MEXÍA, Y.
 7214 bicolor
- MIRANDA BASTOS
 68 subincanum
- MOCIÑO, J. M., & SESSÉ, M.
 3618 angustifolium
 3620 bicolor
 3621 bicolor
 s.n. angustifolium
 s.n. bicolor
- MONTEIRO DA COSTA
 121 grandiflorum
- MULLER, J. V. S.
 s.n. bicolor
- PATIN, C.
 s.n. cacao
- PATINO, V. M.
 22 subincanum
 24 nemorale
- 115 chocoense
 116 nemorale
 117 nemorale
 163 grandiflorum
 169 chocoense var. bullatum?
 171 chocoense var. bullatum
 171A chocoense var. bullatum
 171B chocoense var. bullatum
 s.n. speciosum
- PAVÓN, J.
 617 bicolor
 201 subincanum
 s.n. bicolor
 s.n. sinuosum
- GENTLE, PERCY
 3464 bicolor
- PHILIPSON, W. R., IDROBO, J. M.,
 & FERNÁNDEZ, A.
 1552 glaucum
- PIRES, J. M.
 136 sylvestre
 4340 bicolor
 4343 grandiflorum × obova-
 tum
 4344 grandiflorum × obova-
 tum
 4345 speciosum × sylvestre
 6575 simiarum
- PIRES, J. M., & BLACK, G. A.
 695 speciosum
 740 speciosum
 742 microcarpum
 743 obovatum
 744 grandiflorum
 746 bicolor
 1414 subincanum
 s.n. obovatum
- PIRES, J. M., FRÓES, R. L., &
 SILVA, N. T.
 5886 speciosum
- PIRES, J. M., NILO, T., & SILVA, A.
 4339 obovatum
- PITTIER, H.
 4105 bernouillii
 4194 hylaeum?
 6883 bicolor
 11112 angustifolium
 14016 simiarum
 16142 angustifolium
 s.n. angustifolium
- PITTIER, H., & DURAND, T.
 3925 simiarum
 8536 angustifolium

- PITTIER, H., & TONDUZ, A.
 4074 angustifolium
 POEPPIG, E.
 18 bicolor
 1845 obovatum
 2352 p.p. subincanum
 2352 p.p. obovatum
 2746 p.p. obovatum
 2746 p.p. bicolor
 s.n. bicolor
 s.n. obovatum
 POITEAU, A.
 s.n. subincanum
 PREUSS, P.
 1381 angustifolium
 RANGHEL, A.
 195 subincanum
 REKO, B. P.
 6068 bicolor
 RICHARD, L. C.
 s.n. grandiflorum
 RIEDEL, L.
 1373 grandiflorum
 s.n. grandiflorum
 RIVERO
 1836 subincanum
 ROMERO CASTAÑEDA, R.
 5405 bernouillii subsp. capil-
 liferum
 5500 stipulatum
 s.n. bicolor
 RUÍZ, H., & PAVÓN, J.
 s.n. bicolor
 s.n. sinuosum
 s.n. subincanum
 RUSBY, H. H.
 647 speciosum
 654 speciosum
 SAGOT, P.
 1206 velutinum
 SANDEMAN, C.
 2233 grandiflorum
 SCHOMBURGK, R.
 870 p.p. bicolor
 870 p.p. obovatum
 s.n. grandiflorum
 SCHULTES, R. E.
 3471 bicolor
 3922 bicolor
 6536 subincanum
 6921 obovatum
 8065 grandiflorum
 8178 grandiflorum
 8385 subincanum
 12104 subincanum
 SCHULTES, R. E., BAKER,
 R. E. D., & CABRERA, I.
 18552 subincanum
 SCHULTES, R. E., & BLACK, G. A.
 8146 grandiflorum
 SCHULTES, R. E., & CABRERA, I.
 14140 subincanum
 15116 subincanum
 17005 subincanum
 17775 obovatum
 17780 microcarpum
 17781 grandiflorum
 18695 gileri
 SCHULTES, R. E., & CORDEIRO, E.
 6507 speciosum
 SCHULTES, R. E., & LÓPEZ, F.
 9204 grandiflorum
 SCHULTES, R. E., & SILVA, A.
 8066 speciosum
 SCHULTZE-RHONHOF
 2312 glaucum
 SESSÉ, MOCIÑO, CASTILLO, &
 MALDONADO
 3618 angustifolium
 3620 bicolor
 3621 bicolor
 SIBER
 4 grandiflorum
 s.n. speciosum
 SILVA, J. F.
 143 subincanum
 155 obovatum
 SILVA, A.
 237 subincanum
 317 subincanum
 SIQUEIROS, R.
 4008 grandiflorum
 SMITH, J. DONN.
 6457 simiarum
 7313 simiarum
 7731 simiarum
 SNETHLAGE, E. H.
 300 grandiflorum
 10044b speciosum
 SPRUCE, R.
 97 subincanum
 166 sylvestre
 456 speciosum
 1609 bicolor
 1737 speciosum
 1822 grandiflorum

- s.n. bicolor
 s.n. speciosum
 s.n. sylvestre
 STANDLEY, P. C.
 22317 angustifolium
 36822 simiarum
 37374 bicolor
 37377 simiarum
 79068 angustifolium
 79069 bicolor
 82446 bicolor
 STERN, W., & CHAMBERS, K.
 140 angustifolium
 STEYERMARK, J. A.
 44941 bicolor
 49317 bicolor
 STOCKDALE, J. A.
 s.n. bicolor
 SUCHTELEN, N. J. v.
 s.n. simiarum
 TATE, G. H. H.
 944 subincanum
 TESSMANN, G.
 3433 obovatum
 4079 bicolor
 4115 subincanum
 4928 sinuosum
 5398 speciosum
 s.n. subincanum
 TONDUZ, A.
 4074 angustifolium
 6852 simiarum
 8373 simiarum
 11304 bicolor
 12822 simiarum
 13110 bicolor
 18222 simiarum
 TRAILL, J. W. R.
 59 subincanum
 60 bicolor
 61 obovatum
 62 glaucum
 s.n. bicolor
 TRIANA, J. J.
 5333(-3) bicolor
 s.n. bicolor
 TUERCKHEIM, H. v.
 7824 bicolor
 ULE, E. H. G.
 5030 bicolor
 5637 obovatum
 9609 speciosum
 14448 speciosum
 WEBERBAUER, A.
 6245 bicolor
 WEDEL, H. v.
 681 bernouillii subsp. asclepiadiflorum
 1535 p.p. bernouillii subsp. asclepiadiflorum
 1535 p.p. Lauraceae sp.
 WICKHAM, H. A.
 s.n. grandiflorum
 WILLIAMS, R. O.
 12121 angustifolium
 WILLIAMS, LLEWELYN
 161 obovatum
 230 obovatum
 1076 subincanum
 1233 subincanum
 2149 bicolor
 2401 grandiflorum
 3254 subincanum
 3346 bicolor
 5268 obovatum
 9345 bicolor
 15204 subincanum
 15614 grandiflorum

Collections of *Theobroma cacao* L. Seen

- Acosta Solís, M., 6332, 10724a.
 Allen, Cyril, 880, 881.
 Asplund, E., 13408, 14464, 14583, 14788.
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 Bonpland, A., 1102, s.n.
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Bibliography

- ADANSON, M. 1763. Familles des plantes 2:344, 382.
- ADDISON, G. C., & MIRANDA TAVARES, T. 1951. Observações sobre as espécies do gênero *Theobroma* que ocorrem na Amazônia. Bol Técn. Inst. Agron. Norte, Belém-Pará, 25:1-20, 21 pl.
- ALLEN, PAUL H. 1956. The rain forests of Golfo Dulce. Univ. of Florida Press.
- ALM, JACOBUS. 1785. Plantae surinamenses, in Linnaeus, Amoen. Acad. 8, No. CLXVI, p. 261, ed. Schreber.
- AUBLET, J. B. C. F. 1775. Pl. Guiane. 2:682-689; 4:275, 276.
- BAILLON, H. 1861-62. Etudes organogéniques sur quelques genres de byttneriacées. Adansonia 2:166-181.
- . 1870. Traité du développement de la fleur et du fruit (suite). Adansonia 9:366-348, pl. 5.
- . 1873. Histoire des plantes 4:77-80, 131, figs. 124-129. Paris.
- . 1884. Traité de botanique médicale phanérogamique. Paris.
- BAKER, R. E. D. 1953. Anglo-Colombian cacao collecting expedition. Cacao Res. Rep. 1952, 8-10, Imperial College of Tropical Agriculture, Trinidad.
- . 1961. The Botany of cocoa, in D. H. Urquhart, Cocoa, pp. 7-17.
- BAKER, R. E. D.; COPE, F. W.; HOLLIDAY, P. C.; BARTLEY, B. G., & TAYLOR, D. J. 1954. The Anglo-Colombian Cacao Collecting Expedition. Cacao Res. Rep. 1953, 8-29, Imperial College of Tropical Agriculture, Trinidad.
- BAUHIN, KASPAR. 1623. Pinax theatri botanici, p. 442. Basel.
- BENOIST, R. 1921. Descriptions d'espèces nouvelles de phanérogames. Bull. Mus. Hist. Nat. Paris 27:113.
- BENTHAM, G., & HOOKER, J. D. 1862. Gen. Pl. 1:214-225.
- BERNOULLI, GUSTAV. 1869. Uebersicht der bis jetzt bekannten Arten von *Theobroma*. Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesamnten Naturwissenschaften. Band 24³:1-15, 7 Tafeln. Zürich. 1871. Reprint (15 pp., 7 pl.) issued 1869.
- BERRY, E. W. 1929. Tertiary fossil plants from Colombia, South America. Proc. U.S. Nat. Mus. 75²⁴:8, pl. 1.
- BLACKWELL, ELIZABETH. 1739. A Curious Herbal, vol. 2, London.
- . 1760. Collectio Stirpium . . . (German edition) Centuria 4, pl. 373. Norimbergae.
- BOIS, D. 1937. Les Plantes Alimentaires, IV Les plantes a boissons, [Cacao et Chocolat] pp. 402-437. Paris.
- BONDAR, G. 1924. Cacao Criollo na Bahia. Secret. Agr. Est. Bahia, 1-66, figs.
- . 1938. A cultura de Cacao Bahia. Bol. Técn. Inst. Cacao Bahia, no. 1, pp. 1-205, figs. São Paulo.
- BROWN, ROLAND W. 1946. Alterations in some fossil and living floras. Journ. Washington Acad. Sci. 36:353.
- CAMPOS PORTO, P. 1936. Plantas indigenas e exoticas provenientes da Amazonia, cultivadas no Jardim Botânico do Rio de Janeiro. Rodriguesia 2⁵:135, 136.
- CATESBY, M. 1747. Natural History of Carolina, Florida, and the Bahama Islands. Appendix, London.
- CHATT, Eileen M. 1953. Cocoa, cultivation processing analysis. Economic Crops vol. III, 302 pags. London.

- CHEESMAN, E. E. 1927. Fertilization and Embryogeny in *Theobroma cacao*, L. Ann. Bot. 41:107-126.
- . 1932. The economic botany of Cacao; a critical survey of the literature to the end of 1930. Trop. Agr. (Trinidad), 9³:Sup. pp. 1-16.
- . 1935. The Vegetative Propagation of Cacao. Trop. Agr. (Trinidad) 12⁹:24-246.
- . 1944. Notes on the nomenclature, classification and possible relationships of cacao populations. Trop. Agr. (Trinidad) 21⁸:144-159, map.
- . 1947. Flora of Trinidad and Tobago (Sterculiaceae) 1⁸:491.
- CHEVALIER, AUGUST. 1908. Le Cacaoyer dans l'Ouest Africain in Les Végétaux Utiles d'Afrique tropicale française 4:7-15.
- . 1946. Révision du genre *Theobroma*, Rev. Bot. Appl. 26:265-285. *figs.*
- CIFERRI, R. 1933. Monografia delle varietà, forme e razze di cacao coltivate in San Domingo. Real. Accad. Ital. Mem. Cl. Sci. Fis., Matemat. Nat. IV¹⁸:589-676. Roma.
- CLUSIUS, CAROLUS. 1605. Exoticorum libri decem, . . . item Petri Bellonii Observationes, eodem Carolo Clusio interprete. Cacao Fructus, capit. XXVIII, pp. 55, 56. Antwerp.
- COOK, O. F. 1915. Tribroma, a New Genus Related to Theobroma. Journ. Washington Acad. Sci. 5:287-289.
- . 1916. Branching and Flowering Habits of Cacao and Patashte. Contr. U.S. Nat. Herb. 17:609-625, *pl. 44-54*.
- COPE, F. W. 1940. Agents of pollination in Cacao. Ninth Annual Report on Cacao Research, 1939:13-19. Trinidad.
- . 1940a. Studies in the mechanism of self-incompatibility in cacao, II. Ninth Annual Report on Cacao Research, 1939:19-23. Trinidad.
- . 1959. Incompatibility in *Theobroma cacao*. Report on Cacao Research, 1957-58, pp. 7-17. Trinidad.
- CORREA, PIO. 1926. Dicionario das Plantas uteis do Brasil e dos exóticas cultivadas. 1:360-363. Rio de Janeiro.
- CRISTOBAL, CARMEN L. 1960. Revisión del género Ayenia. Opera Lilloana IV. Tucumán.
- CUATRECASAS, JOSÉ. 1944. Notas a la Flora de Colombia, VI; 5-10, *figs. 1-5*. Cali; *ibidem*, Rev. Acad. Colomb. Cienc. 6:32-37, *figs. 1-5*. Bogotá.
- . 1946. Notas a la Flora de Colombia, VIII. Rev. Acad. Colomb. Cienc. 6:547-549, *figs. 3, 4, pl. III, IV*. Bogotá.
- . 1950. Studies in South American Plants, II. Fieldiana, Bot. 27¹:84-87, *fig. 7*. Chicago.
- . 1952. Notas a la Flora de Colombia, XII. Rev. Acad. Colomb. Cienc. 8:465-488, *fig. 4*. Bogotá.
- . 1953. Une nouvelle espèce de *Theobroma*. Rev. Bot. Appl. 33:562-565, *fig. 1*. Paris.
- . 1956. In Macbride, Flora of Peru, Field Mus. Publ. Bot. 13^{3A}:650-660.
- DAHLGREN, B. E. 1923. Cacao. Field Mus. Bot. Leaf. no. 4, *figs.* Chicago.
- DANDY, J. E. 1957. The Sloane Herbarium, 204-208.
- DECANDOLLE, A. P. 1824. Prodr. Syst. Nat. 1:481-485.
- DECANDOLLE, A. 1874. Calques des dessins de la Flore du Mexique de Moçino et Sessé, qui ont servi des types d'espèces dans le systema ou le prodromus, 1:*pl. 112, 113*. Genève.
- DESCOURTILZ, M. E. 1827. Flore pittoresque et médicale des Antilles. 4:147, *pl. 266*. Paris.
- DIELS, L. 1939. Neue Arten aus Ecuador, II. Notizbl. Bot. Gart. Berlin 14:323-341.

- DIETRICH, DAVID. 1847. Synopsis plantarum seu Enumeratio systematica, vol. 4.
- DON, G. 1831. Gen. Hist. dichlam. pl. 1:521-523, fig. 88.
- DUCKE, ADOLFO. 1925. Plantes nouvelles ou peu connues de la région amazonienne; Genre *Theobroma* L. Arch. Jard. Bot. Rio Janeiro, 4:130-133.
- . 1940. As espécies brasileiras de cacau (gênero *Theobroma* L.), na botânica sistemática e geográfica. Rodriguesia 4¹³:265-276, 7 pl.
- . 1954. As espécies brasileiras do gênero *Theobroma* L. Bol. Técn. Inst. Agron. Norte 28:3-20. (Dez. 1953) Belém-Pará. Rio Janeiro.
- EDLIN, H. L. 1935. A critical revision of certain taxonomic groups of the Malvales. New Phytol., 34:1-20, 122-143.
- EMMERT, EMILY WALCOTT. 1940. The Badianus Manuscript (Codex Barberini, Latin 241, Vatican Library). An Aztec Herbal of 1552. 341 pp., 118 plates. Baltimore.
- ENDLICHER, STEPHAN. 1840. Genera plantarum (Buttneriaceae; pp. 995). Vienna, 1840.
- ERNEHOLM, IVAR. 1948. Historical development and present geographical distribution. Cacao production of South America. Göteborg.
- FAWCETT, W., & RENDLE, A. B. 1926. Fl. Jamaica 5:158-160, fig. 60.
- FOSBERG, F. R.; GARNIER, B. J.; & KÜCHLER, A. W. 1961. Delimitation of the Humid Tropics. Geograph. Rev. 51³:333-347, map.
- FREYTAG, GEORGE F. 1951. A revision of the genus Guazuma. Ceiba, 1⁴: 193-225.
- FRÓES, R. L. 1959. Informações sôbre algumas plantas economicas do Planalto Amazônico. Bol. Técn. Inst. Agron. Norte 35, 113 pp. Belém-Pará.
- GAERTNER, JOSEPH. 1791. De fructibus et seminibus plantarum 2:190, pl. 122.
- GAZET DU CHATELIER. 1940. Recherches sur les Sterculiacées. Rév. Gén. Bot. 52:174-191, 211-233, 257-284.
- GEOFFROY, E. F. 1741. Tractatus de Materia Medica, vol. 2: De Vegetabilibus exoticis, pp. 409-411, Paris.
- GMELIN, J. F. 1791. In Linnaeus, Systema Naturae, ed. 13, 2:1151.
- GÓMEZ DE LA MAZA. 1890. Catálogo de las Periantias Cubanas. Anal. Soc. Esp. Hist. Nat. 19:213-278. Madrid.
- HALL, C. J. J. VAN. 1914. Cocoa, pp. 1-515, 140 figs., London, Macmillan & Co., 1932. Second edition (entitled Cacao), pp. 1-514, 176 figs.
- HARDY, FREDERICK. 1960. Cacao Manual, English edition, Turrialba.
- HART, JOHN HINCHLEY. 1892. Cocoa. pp. 1-77. Port of Spain, Trinidad.
- . 1900. "Cacao," A treatise on the cultivation and curing of "Cacao," pp. 1-117. Trinidad.
- . 1909. The characters of Criollo cacao. West Indian Bull. 9:161,162.
- . 1911. Cacao, a manual on the cultivation and curing of cacao, pp. 1-323. London.
- HEMSLEY, W. B. 1879-1888. Biol. Centr. Am. Bot. 1:133; 4:153.
- HERNÁNDEZ, FRANCISCO. 1651. Rerum Medicarum Novae Hispaniae Thesaurus, seu Plantarum, Animalium, Mineralium Mexicanorum Historia. Rome.
- . 1942. Historia de las Plantas de Nueva España, 3:908-916. México. Translation from the Lincei edition of Rerum Medicarum Novae Hispaniae Thesaurus . . . (1630, 1651).
- HOFFMANN, ANTONIUS. 1765. Potus Chocolatae. Ibidem in Linnaeus Amoen. Acad. 7, No. CXXXVIII, pp. 254-263. 1769. Stockholm.

- HOLDRIDGE, LESLIE R. 1950. Notes on the native and cultivated cacaos in Central America and Mexico. *Cacao Inform. Bull.* 2¹:1-6. Inter-American Institute of Agricultural Sciences.
- . 1950a. Notas sobre los Cacaos silvestres y cultivados en Centro América y México. *Bol. Inform. del Cacao.* 2¹:1-5. Inst. Interam. Cienc. Agrícolas.
- HUBER, J. 1904. Materiaes para a Flora Amazonica. Notas sobre a patria e distribuição geographica das Arvores fructíferas do Pará. *Bol. Mus. Goeldi (Museu Paraense)* 4:392-395.
- . 1906. Materiaes para a Flora Amazonica, VI. Plantas vasculares colhidas e observadas no baixo Ucayali e no Pampa del Sacramento, nos mezes de outubro a dezembro de 1898. *Bol. Mus. Goeldi (Museu Paraense)* 4:510-619.
- . 1906a. Sur l'indigénat du *Theobroma Cacao* dans les alluvions du Purús et sur quelques autres espèces du genre *Theobroma*. *Bull. Herb. Boiss.* II, 6:272-274.
- HUMBOLDT, A., & BONPLAND, A. 1808. *Plant. aequin.* 1:104-106, *pl.* 30, 30b.
- HUMBOLDT, A.; BONPLAND, A.; & KUNTH, K. S. 1823. *Nov. Gen. Sp.* 5:309-317.
- HUNTER, J. ROBERT. 1959. Germination in *Theobroma cacao*. *Cacao* 4¹:1-23.
- HUNTER, J. ROBERT; & BOROUGHS, H. 1961. Effect of temperature on the germination of cacao seed. *Cacao*, 6³:16.
- JUMELLE, HENRI. 1899. Le Cacaoyer, Sa culture et son exploitation dans tous les pays de production. *Ann. Inst. Colon. Marseille* 6:1-211 (botany pp. 1-38, *figs.* 1-17).
- JUSSIEU, A. L. DE. 1789. *Genera Plantarum* 276, 277.
- KARSTEN, H. 1856. *Plantae columbianae.* *Linnaea* 28:447, 448.
- LAMARCK, J. B. A. P. M. 1785. *Encycl. Meth. Bot.* 1:533-535.
- . 1796. *Tabl. Encycl. Meth. Bot.* 2, *pl.* 635.
- LASSER, T., in Pittier et al. 1947. *Catal. Fl. Venez.* 2:139. Caracas.
- LEMÉE, ALBERT. 1952. *Flore Guyane française*, vol. II. Brest.
- LEÓN, JORGE. 1949. Una especie nueva de *Theobroma*. *Bol. Técn.* 2:1-3, *figs.* Inst. Interam. Cienc. Agrícolas, Turrialba.
- . 1950. Curso de Taxonomía. Género *Theobroma* L. Grupo B. Inst. Interam. Cienc. Agrícolas (mimeograph).
- . 1954. A note on cacao "lagarto" or pentagona. Fifth meeting of the Inter-American technical committee on Cacao. *Cacao* 3⁴:9.
- . 1960. Taxonomy of Cacao and related genera (Systematics of the genus *Theobroma*), in Frederick Hardy's *Cacao Manual*, 307-324.
- LIGNIER, O., & LEBEY, R. 1904. Liste des Plantes vasculaires que renferme l'Herbier général de l'Université et de la Ville de Caén (suite). *Bull. Soc. Linn. Normandie* V, 8:263. Caen.
- LINNAEUS, C. 1737. *Genera Plantarum*, 351.
- . 1737. *Hortus Cliffortianus, plantae exhibens, quas in hortis tam vivis quam siccis Hartecampi in Hollandia coluit vir nobilissimus et generosissimus Georgius Clifford.* Amsterdam.
- . 1749. *Materia medica, liber 1, de Plantis.* Stockholm.
- . 1753. *Species Plantarum*, 2:782.
- . 1754. *Genera Plantarum*, ed. 5, 340. Stockholm.
- . 1764. *Species Plantarum*, ed. 3, 1100.
- . 1767. *Systema Naturae*, ed. 12, reformata 2:508.
- . 1770. *Systema Naturae*, ed. 13, 2:508.

- LLANO GÓMEZ, ENRIQUE. 1947. Cultivo del Cacao. 150 pp., several plates in color. Publ. Minist. Economía Nacional. Bogotá.
- LLANO BUENAVENTURA, MANUEL. 1958. La Limofytia freática, máximo biológico regional en el mundo y óptimo medio estacional del cacaotero, *Theobroma cacao* L. Medellín.
- MARTIUS, C. E. P. VON. 1830. Ueber den Cacao und die ihn liefernden Pflanzen-Arten. Buchner's Repertorium der Pharmacie, 35:1-24; *ibidem*, Linnaea: Litt.-Bericht. 31-33. 1831.
- . 1831. Reise in Brasilien, 3:1127.
- MCCREARY, C. W. R.; McDONALD, J. A.; MULOON, V. I., & HARDY, F. 1943. The Root System of Cacao. Trop. Agr., [Trinidad] 20:207-220.
- MERIAN, MARIA SIBILLA. 1705. Dissertatio de generatione et metamorphosibus insectorum surinamensium. 26, pl. 26. Amsterdam.
- MILDBRAED, J. 1931. Plantae Tessmannianae Peruvianae, VIII. Notizbl. Bot. Gart. Berlin, 11:135-146.
- MILLER, PHILIP. 1752. The Gardeners Dictionary, 6th edition, London.
- . 1754. The Gardeners Dictionary. Abridged fourth edition. London.
- . 1768. The Gardeners Dictionary, 8th edition, London.
- MIRANDA, F. 1952. La Vegetación de Chiapas, 1:222-226; 2:187. Tuxtla Gutiérrez.
- MORA URPI, JORGE. 1958. Notas sobre el posible origen y la variabilidad del Cacao cultivado en América Tropical. Turrialba 8¹:34-43.
- MORRIS, D. 1882. Cacao: how to grow and how to cure it, pp. 1-45. Jamaica.
- MUELLER, WOLF. 1951. Bibliographie des Kakao, seiner Geschichte, Kultur, Verwendung, Verarbeitung und wirtschaftlichen Bedeutung, pp. 1-120. -Verlag Gordian, Hamburg.
- . 1957. Seltsame Frucht Kakao (Geschichte des Kakaos und der Schokolade), pp. 1-224, 28 pl. Verlag Gordian, Hamburg.
- MYERS, J. G. 1930. Notes on wild Cacao in Surinam and in British Guiana. Kew Bull. 1930, no. 1:1-10, pl. i, ii.
- PISO, W. 1658. De Indiae Utriusque re Naturali et Medica Libri Quatordecem. Capt. XVIII:197. Amsterdam.
- PITTIER, HENRI. 1902. ¿Es el cacaotero indígena en Costa Rica? Bol. Inst. Físico-Geograf. Costa Rica 2²⁰:193-196. San José.
- . 1914. Malvales novae Panamenses. Repert. Sp. Nov. Fedde 13:312-320.
- . 1925. L'origine hybride des Cacaoyers cultivés. With "Observations de A. Chevalier." Rev. Bot. Appl. 5⁵²:908-915.
- . 1926. Manual de las Plantas Usuales de Venezuela. [Cacao] pp. 147-149. Caracas.
- . 1930. A Propos des Cacaoyers spontanés. Rev. Bot. Appl. 10¹¹⁰:777-781.
- . 1932. El Cacaotero. Apuntes históricos y botánicos. Bol. Soc. Venez. Cienc. Nat. 1:170-184.
- . 1957. Ensayo sobre Plantas Usuales de Costa Rica, ed. 2, rev. 71-73. Publ. Univ. Costa Rica, Ser. Cienc. Nat., No. 2. San José.
- PITTIER, HENRI; DUCKE, A., & CHEVALIER, A. 1926. L'Origine géographique et botanique des Cacaoyers et l'utilité de leur greffage. [Pittier: A Propos des Cacaoyers de Venezuela 345-346; Ducke: Les Theobroma du Brésil 346-348; Chevalier: A Propos de greffage du Cacaoyer 348, 349.] Rev. Bot. Appl. 6⁵⁸:344-349, 2 pl.
- PLUKENET, L. 1696. Almagestum botanicum 40, t. 268, f. 3.

- PLUMIER, CHARLES. 1693. Description des plantes de l'Amerique, avec leurs figures. Paris.
- POIRET, J. L. M. 1811. In Lamarek, Encycl. Méth. Bot. Suppl. 2:7, 8.
- . 1823. In Lamarek, Tabl. Encycl. Méth. Bot. 3:196.
- POUND, F. J. 1938. Cacao and witchbroom disease of South America. Port of Spain, Trinidad.
- . 1943. Certain aspects of Agriculture in Colombia with special reference to the production of cacao. Report to the Ministry of National Economy. Bogotá. (Mimeograph.)
- PREUSS, PAUL. 1901. Expedition nach Central und Südamerika 1899/1900. Verlag des Kolonial—Wirtschaftlichen Komitees. Berlin.
- . 1902. Le Cacao, sa Culture et sa préparation (French translation). Bull. Soc. Études Colon. de Belgique, 2-3:53-134 and 205-256.
- PRITZEL, G. A. 1872. Thesaurus Literaturae Botanicae. 577 pp. Lipsiae.
- RAY, J. 1688. Historia Plantarum 2:1670, 1671. London.
- . 1710. Methodus Plantarum. Amsterdam, 1710; London, 1733.
- REHDER, ALFRED. 1912. The Bradley Bibliography, vol. II, Dendrology, part II, p. 539. Cambridge, Mass.
- RENDLE, A. B. 1923. George Clifford's herbarium and the Hortus Cliffortianus. Journ. Bot. 61:114-116.
- RICHARD, ACHILLE. 1845. Essai d'une Flore de L'Ile de Cuba, 1:183, 184. Paris.
- . 1845a. Fanerogamia o Plantas Vasculares, in Sagra, Hist. Cuba 73. Madrid.
- RIVER STATE EXPERIMENT STATION. 1960 report (in mimeograph).
- ROMBOUTS, J. E. 1948. Theobroma Saltzmanniana. Kew Bull. 1948:104-106.
- SAGOT, P. 1881. Catalogue des Plantes de la Guyane Française. Ann. Sci. Nat. VI, Bot. 11:134-180.
- SALISBURY, RICHARD A. 1796. Prodromus stirpium in horto ad Chapel Allerton vigentium, pp. I-VIII, 1-422. London.
- SAVAGE, SPENCER. 1945. A catalogue of the Linnaean Herbarium. London.
- SCHREBER, JOHANN D. C. VON. 1791. In Linnaeus, Genera Plantarum, ed. 8, 2:513.
- SCHULTES, RICHARD EVANS. 1958. A synopsis of the genus Herrania. Journ. Arn. Arb., 39³:216-278, 17 plates.
- SCHUMANN, KARL. 1886. Vergleichende Blütenmorphologie der cucullaten Sterculiaceen. Jahrb. Bot. Gart. Berlin, 4:286-332, pl. III, IV.
- . 1886. In Martius, Fl. Bras. 12³.
- . 1890. Sterculiaceae, in Engler & Prantl, Die Natürlichen Pflanzenfamilien, 3⁶.
- SLOANE, HANS. 1696. Catalogus Plantarum quae in Insula Jamaica sponte proveniunt . . . seu Prodromi Historiae Naturalis Jamaicae pars Prima. London.
- . 1725. A voyage to . . . Jamaica, with the natural history, 2:15. pl. 160. London.
- SMITH, JOHN DONNELL. 1898. Polypetalae, in Pittier, Primitiae Florae Costaricensis. Anal. Inst. Físico-Geográf. Costa Rica 9:96.
- SORIA V., JORGE. 1959. Notes on the variability of cacao types in some Nicaraguan plantations and comments on their genetic constitution. Cacao, 4²:1, 2.
- . 1961. Anotaciones sobre un viaje a las zonas productoras de cacao en México (Marzo 6-18, 1961), pp. 1-18. Turrialba (mimeograph).
- SPRAGUE, T. A. 1955. Theobroma cacao L. Early illustrations and date of introduction into cultivation in Europe. Cacao 3⁷:2, 3. Turrialba.

- SPRENGEL, KURT. 1826. In Linnaeus, Syst. Veg., ed. 16, 3:330-332. Göttingen.
- STAHEL, GEROLD. 1918. Ueber die Inflorescenzen von *Theobroma Cacao* Linn. und *Theobroma bicolor* Humb. und ihre Umformung unter den Einfluss des Krülloten schimmels (*Marasmius perniciosus* Stahel). Ann. Jard. Bot. Buitenzorg 30 (II, vol. 15):95-114. *Tafeln 14-20*.
- . 1928. Beiträge zur Kenntniss der Blütenbiologie von Kakao, *Theobroma cacao* L. Verhandl. Akad. Wetens. Amsterdam, Afd. Naturk. 25⁶.
- STANDLEY, PAUL C. 1923. Trees and shrubs of Mexico. Contr. U.S. Nat. Herb., 23³: 805-808.
- . 1937. Flora of Costa Rica, part 2. Field Mus. Publ. Bot. 18²: 687-689.
- STANDLEY, PAUL C., & STEYERMARK, JULIAN A. 1949. Flora of Guatemala. Fieldiana, 24⁶: 421-427.
- STOKES, JONATHAN. 1812. A Botanical Materia Medica, vol. 8.
- SWEET, ROBERT. 1830. Hortus Britannicus or Catalogue of Plants, . . . London.
- TOURNEFORT, J. P. 1700. Institutiones Rei Herbariae, 1:660; 3: *Tab. 444*.
- TRIANA, J., & PLANCHON, J. E. 1862. Prodromus Florae Novogranatensis 1:208, 209. Paris.
- TROLL, W. 1954, 1957. Praktische Einführung in die Pflanzenmorphologie. 2 vols. Jena.
- TUSSAC, F. R. de. 1808. Flora Antillarum, seu Historia Generalis, Botanica . . . 1:101. Paris.
- URQUHART, D. H. 1961. Cocoa. Trop. Agr. Series, Longmans, Green, & Co., Ltd. London.
- VOIGT, F. S. 1828. Plantarum rariorum in horto Belvederense cultarum, in Sylloge Plantarum Novarum, 50-55. Ratisbonae (Regensburg).
- WEINMANN, JOHANN WILHELM. 1739. Phytanthoza iconographia. 2:1-11, *pl. 277, 278*. Amsterdam.
- WILDEMAN, EMILE DE. 1895. Un *Theobroma* nouveau. Bull. Herb. Boiss. 7:957, 958, *pl. 11*.
- . 1902. Les Plantes Tropicales de Gran Culture. [Le Cacao] pp. 81-119, *figs.* Bruxelles.
- WILDENOW, C. L. 1802. In Linnaeus, Species Plantarum, ed. 4, 3²:1422.
- WILLIAMS, LEWELYN. 1936. Woods of Northeastern Peru. Field Mus. Publ. Bot. 15:321-325.
- WILLAMAN, J. J., & SCHUBERT, B. G. 1961. Alkaloid-bearing plants and their contained alkaloids. U.S. Dept. Agr. Tech. Bull. 1234. Washington, D.C.



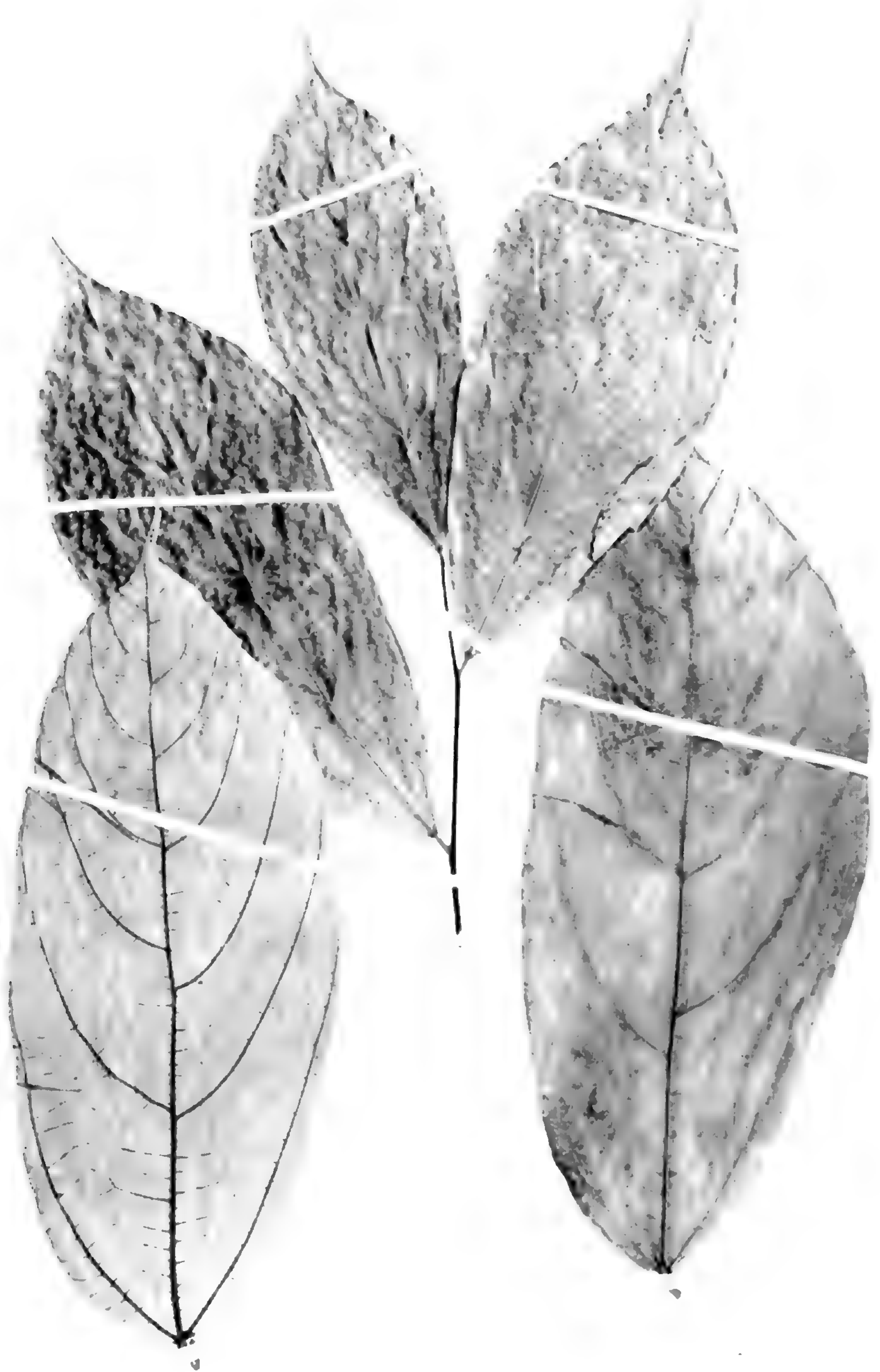
Theobroma sylvestre Mart., lectotype at Munich (photo FM 19644).



Theobroma speciosum Willd. ex Spreng., isotype formerly at Berlin-Dahlem; identical with the holotype in the Willdenow Herbarium (photo FM 9640).



Theobroma speciosum Willd. ex Spreng., isotype of *T. quinquenervia* Bern., Spruce 1737 at Berlin-Dahlem (photo FM 9639)



Theobroma glaucum Karstén, holotype at Vienna (photo FM 32205).



Theobroma bernouillii subsp. *capilliferum* Cuatr., in the rain forest, Pacific coast, Colombia
(photo Cuatrecasas C 2202).



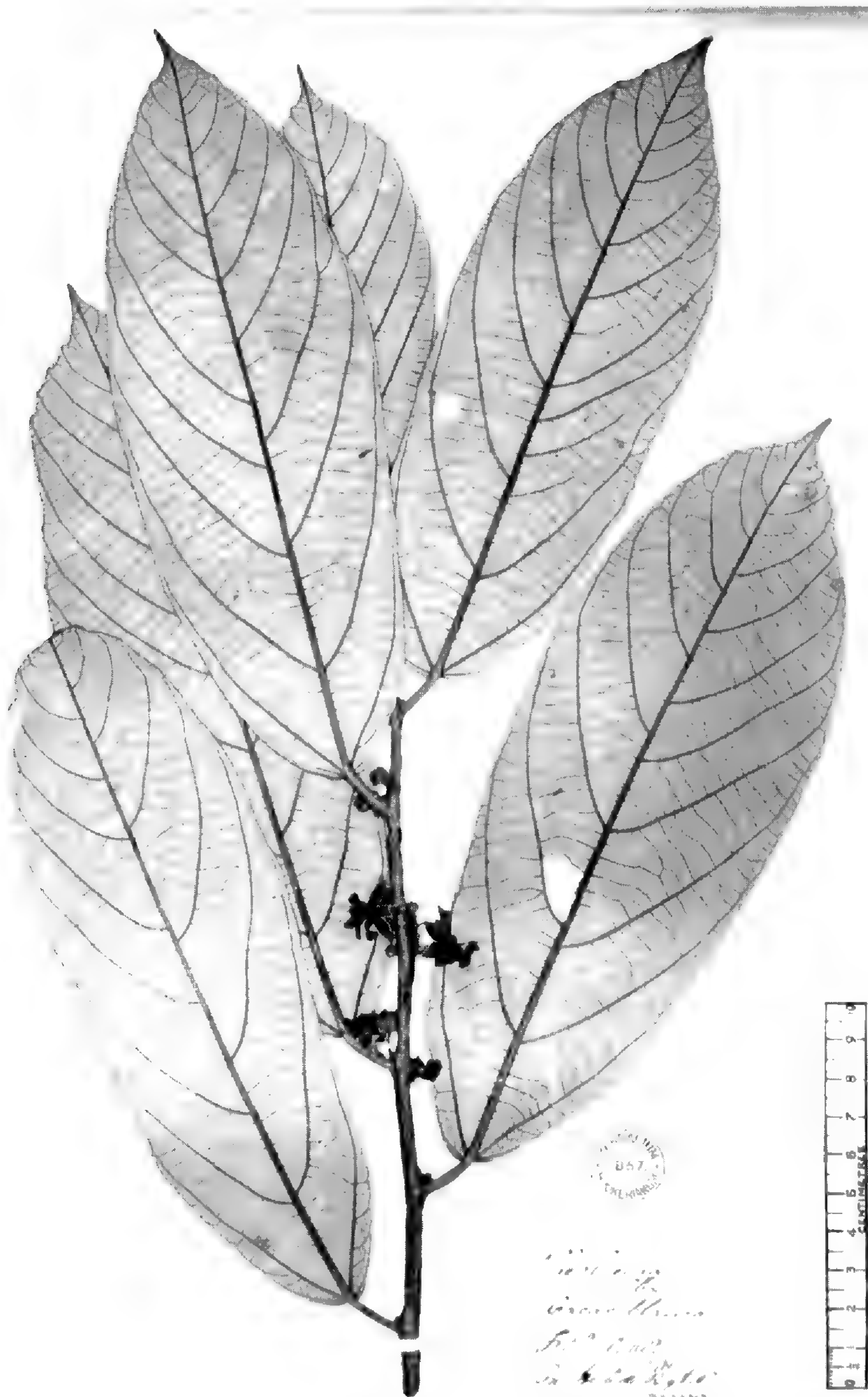
Theobroma cacao subsp. *platanifolium* (Chev.) Cuatr. cultivar "melonado" at San José del Guaviare, Colombia (photo Cuatrecasas C-1500)



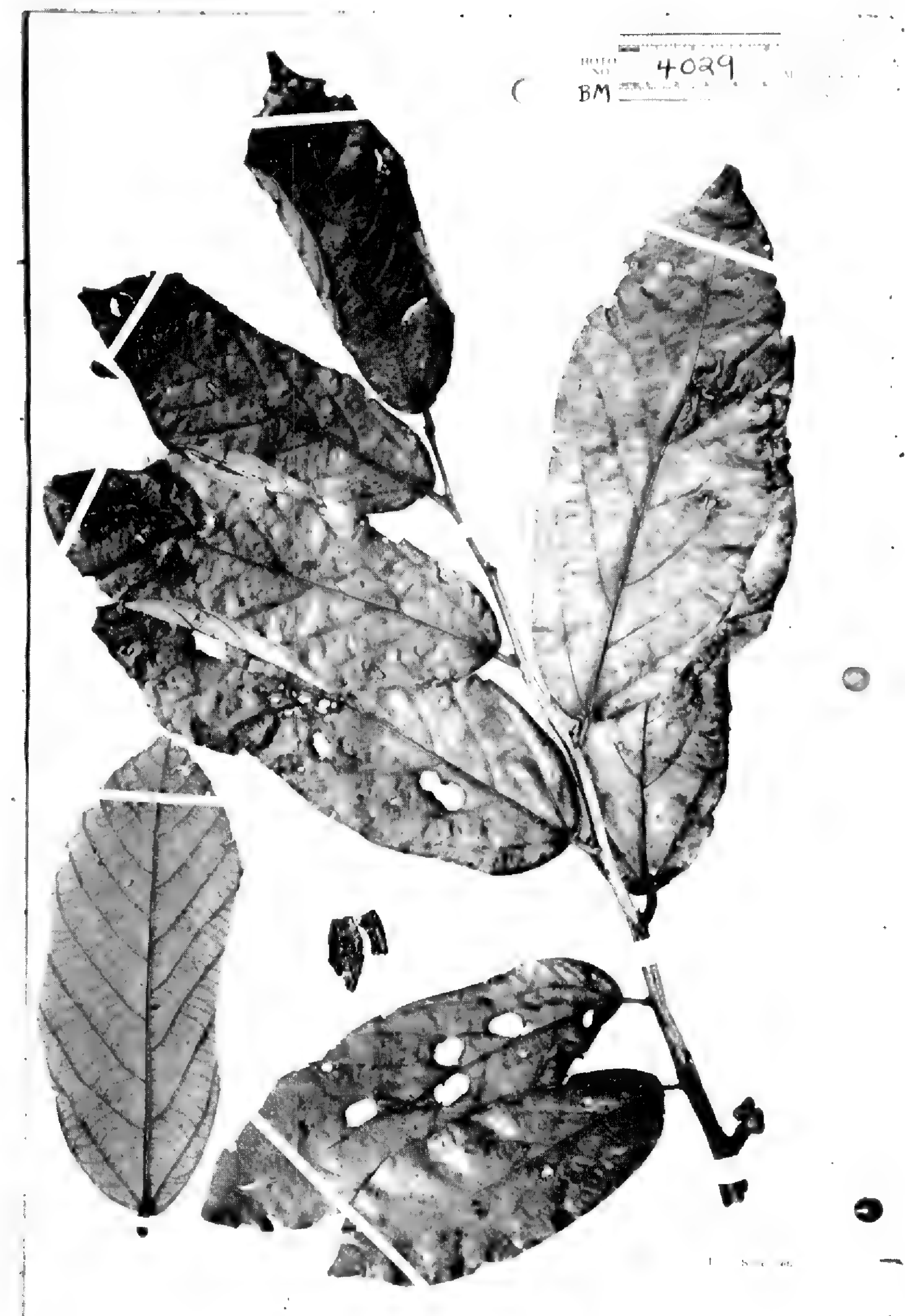
Theobroma cirmolinae Cuatr.; caulinar inflorescences, on trunk, with opening buds and yellow flowers, at the western Andes in El Valle, Colombia (photo Cuatrecasas C-2132).



Theobroma grandiflorum (Spreng.) Schum., lectotype of *T. macrantha* Bern. and neotype of *T. grandiflorum* Schum., Spruce 1822, at Munich (photo CNHM 40705).



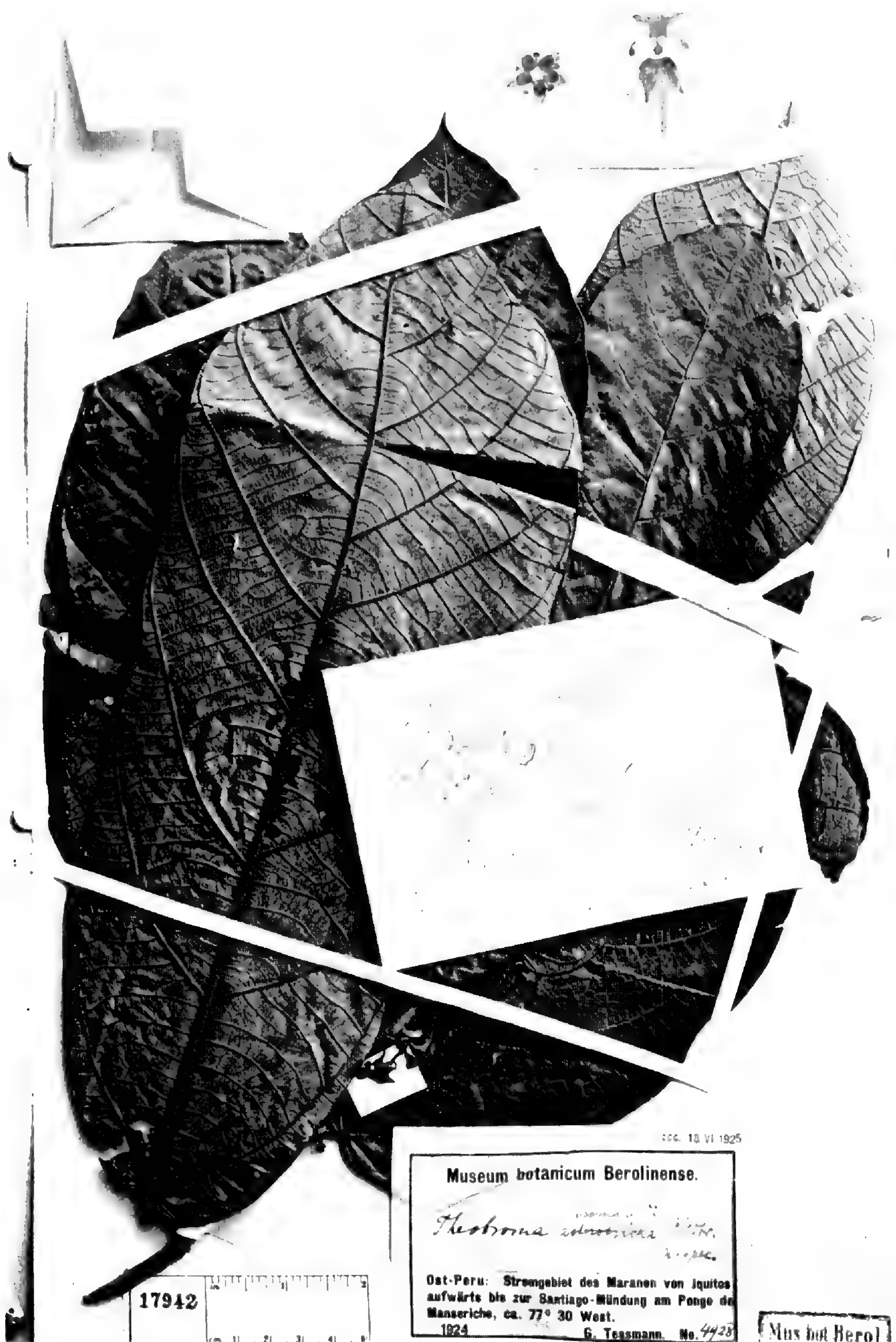
Theobroma subincanum Mart., holotype of *T. ferruginea* Bern. at Kew, collect. R. & P.
(photo Royal Botanic Gardens, Kew).



Theobroma subincanum Mart., lectotype of *Cacao sylvestris* Aublet in the British Museum (photo BM 4029, Mo. Bot. Gard.).



Theobroma subincanum Mart., syntype (part) of *Cacao guianensis* Aublet, in the British Museum (photo BM 4028, Mo. Bot. Gard.).



Theobroma sinuosum Pavón ex Huber; type of *T. tessmannii* Mildbr. formerly at Berlin-Dahlem (photo FM 17942).

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